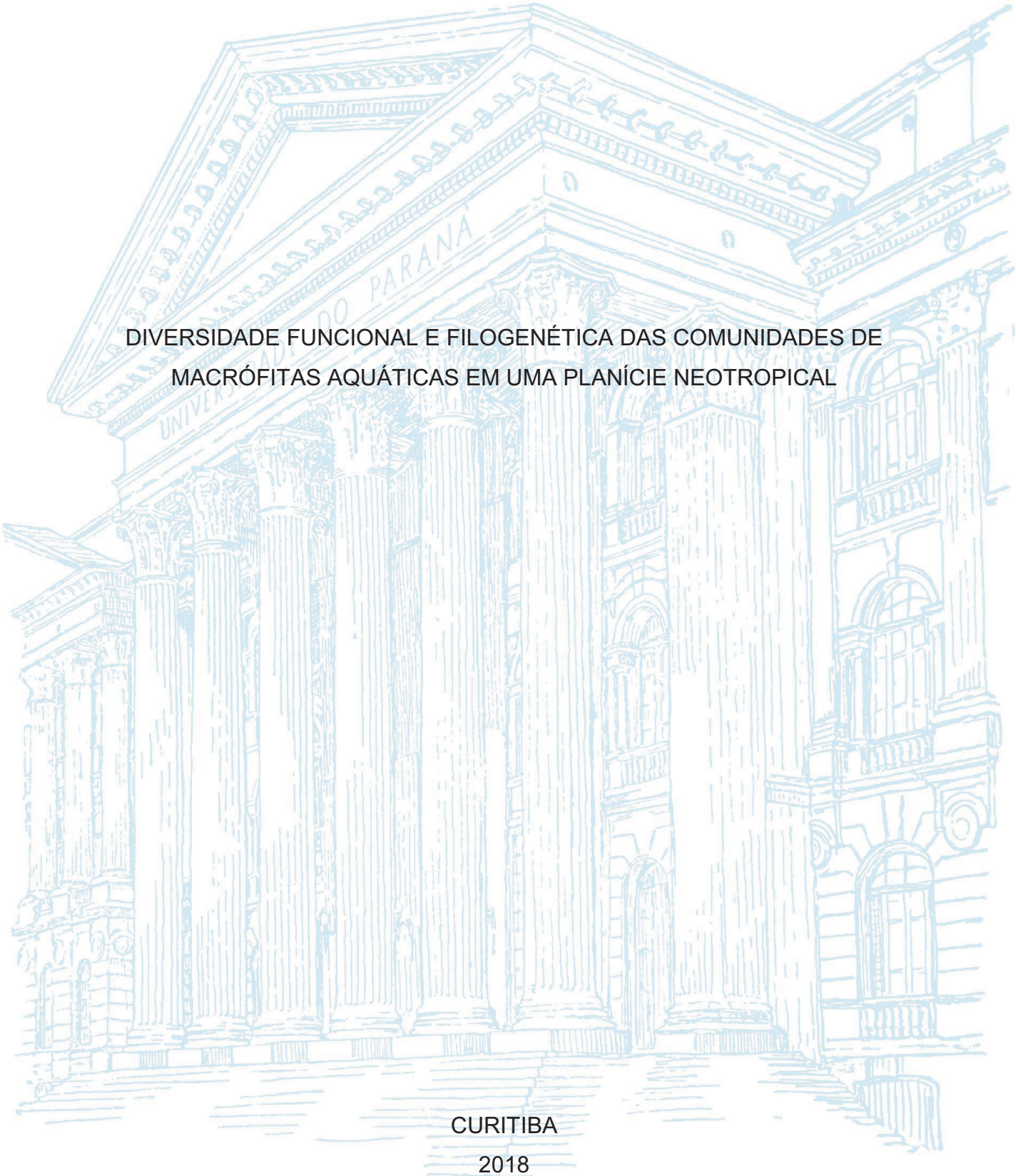
UNIVERSIDADE FEDERAL DO PARANÁ

SUELEN CRISTINA ALVES DA SILVA PERETO



DIVERSIDADE FUNCIONAL E FILOGENÉTICA DAS COMUNIDADES DE MACRÓFITAS AQUÁTICAS EM UMA PLANÍCIE NEOTROPICAL

CURITIBA

2018

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DIVERSIDADE FUNCIONAL E FILOGENÉTICA DAS COMUNIDADES DE MACRÓFITAS AQUÁTICAS EM UMA PLANÍCIE NEOTROPICAL

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutora em Ciências Biológicas área de concentração Ecologia e Conservação.

Orientador: Prof. Dr. Andre Andrian Padial
Coorientador: Prof Dr. Guilherme D. S. Seger

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **SUELEN CRISTINA ALVES DA SILVA PERETO** intitulada: **DIVERSIDADE FUNCIONAL E FILOGENÉTICA DAS COMUNIDADES DE MACRÓFITAS AQUÁTICAS EM UMA PLANÍCIE NEOTROPICAL**, após terem inquirido a aluna e realizado a avaliação do trabalho, são de parecer pela sua Aprovação no rito de defesa.

A outorga do título de doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 29 de Junho de 2018.

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Presidente da Banca Examinadora

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Um trabalho nunca é feito por uma pessoa só. Apenas represento cada um de vocês nesse momento!

"Confia no Senhor e faze o bem; habitarás na terra, e verdadeiramente serás alimentado.
Deleita-te também no Senhor, e te concederá os desejos do teu coração.
Entrega o teu caminho ao Senhor; confia nele, e ele o fará".
(Salmos 37:3-5 NVI)

"Trust in the Lord, and do good; so shalt thou dwell in the land, and verily thou shalt be fed.
Delight thyself also in the Lord: and he shall give thee the desires of thine heart.
Commit thy way unto the Lord; trust also in him; and he shall bring it to pass."
(Psalm 37:3-5 KJV)

RESUMO

O papel da diversidade funcional e filogenética no entendimento das respostas das comunidades ecológicas aos gradientes ambientais tem sido um dos principais alvos das pesquisas ecológicas. A diversidade funcional estima a faceta da biodiversidade relacionada com a variedade de características morfológicas, fisiológicas e ecológicas das espécies – os chamados traços funcionais. Dessa forma, a similaridade entre espécies é estimada considerando a sua influencia no funcionamento dos ecossistemas. A diversidade filogenética por sua vez, considera as relações de parentesco entre as espécies, refletindo sob a diversidade da história evolutiva dos clados. O presente estudo teve por objetivo avaliar a variação espacial e temporal da diversidade funcional e filogenética das comunidades de macrófitas aquáticas na Planície de Inundação do Alto Rio Paraná (PIARP). Essa região é composta por três grandes subsistemas (rios), diferentes entre si em relação às características limnológicas, geomorfológicas e biológicas. Utilizamos de um banco de dados de ocorrências de macrófitas aquáticas, assim como de variáveis limnológicas, ao longo de 11 anos de monitoramento de um projeto ecológico. Além desses dados, realizamos uma coleta pontual na PIARP para fins de mensuração intensiva de traços funcionais de tais táxons. Em virtude da efetiva e intensa propagação vegetativa de macrófitas aquáticas consideramos diferenças individuais por coletas de módulos. Nesse caso, cada módulo é definido como a menor porção repetida contendo folha, caule e raiz. Com o objetivo de representar a variabilidade nos traços funcionais de cada táxon coletamos cinco módulos por táxon (prefencialmente em bancos diferentes). Em cada módulo, avaliamos 17 traços funcionais dos 76 táxons de macrófitas aquáticas registradas na PIARP ao longo de 11 anos. Nossos objetivos foram 1) analisar a variação espacial na composição funcional das comunidades de macrófitas aquáticas (capítulo 1); 2) analisar e explicar padrões temporais na diversidade funcional das comunidades de macrófitas aquáticas ao longo de 11 anos (capítulo 2) e, 3) identificar se clados filogenéticos das macrófitas aquáticas são explicados por gradientes ambientais considerando análises em diferentes escalas (capítulo 3). Nossos resultados indicaram que apesar de uma clara variação taxonômica, as comunidades de macrófitas aquáticas apresentam pouca diferença na composição funcional entre os subsistemas. Ao longo dos 11 anos de monitoramento, somente a riqueza funcional teve um padrão de aumento monotônico ao longo dos anos. Provavelmente tal resultado foi afetado por um viés de identificação taxonômica, pois houve maior precisão na identificação somente nos últimos anos do monitoramento. Apesar disso, a flutuação na diversidade funcional foi explicada por preditores ambientais, principalmente aqueles relacionados com a dinâmica do regime hidrológico. A estruturação filogenética das comunidades de macrófitas aquáticas dependeu da escala da análise. Este estudo permitiu maior conhecimento das causas de variação da biodiversidade da flora aquática da PIARP assim, como avanços nos estudos relacionados às respostas dos papeis funcionais e filogenéticos aos gradientes ambientais de comunidades de macrófitas aquáticas.

Palavras-chave: Gradiente ambiental. Homogeneização. Índices funcionais. Preditores ambientais. Escala espacial.

ABSTRACT

One of the main goals of community ecology is to understand the response of functional and phylogenetic diversities to environmental gradients. Functional diversity evaluates the facet of biodiversity related to the variety of morphological, physiological and ecological characteristics of the species - the so-called functional traits. Thus, species similarity is estimated considering its influence on ecosystems functioning. Phylogenetic diversity, on the other hand, considers species kinship relations, reflecting a diversity of clades in the evolutionary history. The objective of this study was to evaluate the spatial and temporal variation of functional and phylogenetic diversity of aquatic macrophyte communities in the Upper Paraná River Floodplain (UPRF). This region is composed of three great subsystems (rivers), different from each other in relation to their limnological, geomorphological and biological characteristics. We used a database of aquatic macrophytes occurrences, as well as limnological variables, over 11 years of a long-term ecological project. In addition to these data, we performed a snapshot sampled in the UPRF for an intensive measurement of taxa functional traits. Due to the effective and intense vegetative propagation of aquatic macrophytes, we consider individual differences by sampling modules. In this case, each module is defined as the minor repeating portion containing leaf, stem and root. In order to represent the variability of functional traits for each taxon, we sampled five modules per taxon (preferentially at different stands). In each module, we evaluated 17 functional traits of the 76 taxa of aquatic macrophytes registered in the UPRF over 11 years. Our objectives were 1) to analyze the spatial variation in the functional composition of the aquatic macrophytes communities (chapter 1); 2) to analyze and explain temporal patterns in the functional diversity of aquatic macrophytes communities over 11 years (Chapter 2); and 3) to identify if phylogenetic clades of aquatic macrophytes are explained by environmental gradients considering analyzes at different scales (chapter 3). Our results indicated that despite a clear taxonomic variation, aquatic macrophyte communities poorly differ among subsystems regarding functional composition. Over the 11 years, only the functional richness had a monotonic increase pattern. Probably, this result was affected by a taxonomic identification bias, since there was greater precision in the identification only in the last years of the monitoring. Despite this, fluctuation in functional diversity was explained by environmental predictors, especially those related to the dynamics of hydrological regime. The phylogenetic structuring of the aquatic macrophyte communities depended on the scale of the analysis. This study allowed a better understanding of aquatic flora variation causes in the UPRF as well as advances in studies related to functional and phylogenetic role responses to environmental gradients of aquatic macrophyte communities.

Keywords: Environmental gradient. Homogenization. Functional indexes.

Environmental predictors. Spatial scale.

SUMMARY

THESIS PRESENTATION

This thesis is composed of three scientific papers elaborated over four years of PhD graduation in the post-graduation program "Ecologia e Conservação" of "Universidade Federal do Paraná" – Brazil. The three chapters containing scientific content were developed and are formatted according to the scientific journal chosen for publication. Chapter one is formatted as a short communication for submission to the *Aquatic Ecology* journal (classification according to the Brazilian agency CAPES: Qualis B1), and has as main objective investigate the spatial differences on the functional composition of aquatic macrophytes communities sampled in fifteen lakes from three subsystems (considered by many previous studies as ecoregions) of the Neotropical floodplain "Upper Paraná River floodplain" (UPRF). The second chapter is formatted and already in review in *Freshwater Biology* journal (classification according to the Brazilian agency CAPES: Qualis A1), and has as main objective describe and explain functional diversity variation of aquatic macrophytes communities over 11 years in the UPRF. The third chapter is formatted in accordance to *Diversity and Distributions* journal (classification according to the Brazilian agency CAPES: Qualis A1) and has as main objective analyze if the enviromental gradients drive the distribution of phylogenetic clades of aquatic macrophytes. In this case, we analyzed the phylogenetic and taxonomic community structure according to environmental gradients over time. Beyond these three chapters, this thesis is also composed by an introductory article (in Portuguese and in English) for scientific divulgation, characterized in a non-formal scientific language. This article will be disclosed in a local online newspaper promoted by the post-graduate program in "Ecologia e Conservação", in order to spread scientific novelty to non-academic community and undergraduate students.

ARTICLE FOR SCIENTIFIC DIVULGATION

“BIODIVERSITY OF AQUATIC PLANTS: WHAT DOES IT MEAN AND WHY IS IT IMPORTANT?”

“Biodiversidade de plantas aquáticas: o que significa e por que é importante?”

“Biodiversity of aquatic plants: what does it mean and why is it important?”

“Biodiversidade de plantas aquáticas: o que significa e por que é importante?”

Suelen Cristina Alves da Silva Pereto

Andre Andrian Padial

Aquatic plants (also called “aquatic macrophytes”, see IBP, 2016) are eye witness plants that inhabits from shallow swamp to truly aquatic areas (Weaner & Clements, 1983). Aquatic plants have a great number of species that are able to survive in either fresh or brackish waters, and some can live in both wet and drought conditions. The high tolerance to variable conditions is resultant of an evolutive process. Aquatic plants were evolved from terrestrial plants that returned to the aquatic environment (Sculthorpe, 1967). This resulted in unique morphological, anatomic and physiologic adaptations (Esteves, 1998). Maybe, the most noteworthy adaptation is an intense presence of cells that store air. This reserve favors fluctuation, allowing aquatic plants to stand even when totally submersed in the water body (Gunawardena *et al*., 2001). Given the high variability of forms and functions,

Plantas aquáticas (também conhecidas como “macrófitas aquáticas”, veja IBP, 2016) são plantas visíveis a olho nú que habitam desde ambientes brejosos até totalmente aquáticos (Weaner & Clements, 1983). Plantas aquáticas possuem um grande número de espécies que são capazes de sobreviver a água doce ou salgada e algumas podem viver em condições tanto seca ou úmida. A alta tolerância a condições variáveis é resultado de um processo evolutivo. Plantas aquáticas evoluíram de plantas terrestres que retornaram ao ambiente aquático (Sculthorpe, 1967). Isso resultou em adaptações únicas morfológicas, anatômicas e fisiológicas (Esteves, 1998). Talvez a adaptação mais importante seja a presença de células que reservam ar. Essa reserva favorece a flutuação, permitindo a permanência das plantas aquáticas mesmo quando totalmente submersas na coluna d’água (Gunawardena *et al*., 2001).

aquatic plants are usually classified in groups that are different considering their role in the surrounding environment (Esteves, 1998; Beklioglu & Moss, 1996). Also, the different groups may be affected by different environmental features (flood, drought, eutrofication, etc) allowing researches to understand why a certain plant inhabits a certain aquatic habitat (Gitay & Noble, 1997; Murphy et al., 2003).

A well used classification of aquatic plants is the one proposed by Pedralli (1990) which classify them in the following life forms: 1) fixed submersed, 2) free submersed, 3) fixed floating, 4) free floating, 5) emergent, 6) amphibious and 7) epiphyte (see their forms in Fig. 1). Fixed submersed are those that have their roots fixed to the underwater soil and live most of their life entirely submersed. Free submersed are those that also are entirely underwater, but roots are not fixed in the soil. Thus, such plants are free to move according to the water flow. Fixed floating are those with fixed roots in underwater soil, but leaves float in water surface. Free floating, such as free submersed, also moves according to water flow. However, only roots are submersed, while leaves and flowers float in water surface. Emergent plants are those that only live in the margin, because roots must be fixed in

Devido à alta variabilidade de formas e funções, plantas aquáticas são usualmente classificadas em grupos que diferem considerando suas importâncias para o ambiente ao seu redor (Esteves, 1998; Beklioglu & Moss, 1996). Da mesma forma, os diferentes grupos podem ser afetados por diferentes características ambientais (cheia, seca, eutrofização, etc) permitindo os pesquisadores a entender o porquê que certas espécies ocorrem em certos ambientes aquáticos (Gitay & Noble, 1997; Murphy et al., 2003).

Uma classificação muito usada de plantas aquáticas é a proposta por Pedralli (1990) o qual as ordenou de acordo com as formas de vida: (1) submersa fixa, (2) submersa livre, (3) flutuante fixa, (4) flutuante livre, (5) emergente, (6) anfíbia e (7) epífita (veja suas formas na Fig.1). Submersa fixa são aquelas que possuem raízes fixas ao solo do corpo d'água e, vivem a maior parte de sua vida inteiramente submersa. Submersa livre são aquelas que da mesma forma estão inteiramente na coluna d'água submersas, mas com suas raízes não fixadas ao solo. Dessa forma, tais plantas são livres para se movimentar de acordo com o fluxo d'água. Fixas flutuantes são aquelas com raízes fixas ao solo do corpo d'água, mas com folhas que flutuam na superfície d'água. Flutuantes livres, assim como submersas

the soil, and leaves and flowers must be above water, at least for some time. Amphibious has a similar form of emergent, and the difference is that amphibious can live with or without being submersed. These plants are very tolerant to droughts, and can even be confounded with terrestrial plants. On the other hand, they are also able to live underwater for a very long time, different to terrestrial plants. Lastly, epiphytes are those that grow above other aquatic plants, which can be any of the other life forms described above.

livres, também se movimentam de acordo com o fluxo d'água. Entretanto, apenas as raízes são submersas enquanto folhas e flores flutuam na superfície d'água. Plantas emergentes são aquelas que apenas vivem na margem devido às raízes serem fixas no solo e as folhas e flores ficam acima da superfície da água, pelo menos por um tempo. Anfíbias possuem uma forma similar às emergentes e a diferença é que as anfíbias podem viver sendo ou não submersas. Essas plantas são muito tolerantes à secas e podem ser confundidas com plantas terrestres. Em contrapartida, elas também são capazes a viver na coluna d'água por muito tempo, diferente das plantas terrestres. Por fim, epífitas são aquelas que crescem acima de outras plantas aquáticas, as quais podem ser quaisquer outras formas de vida descritas acima.

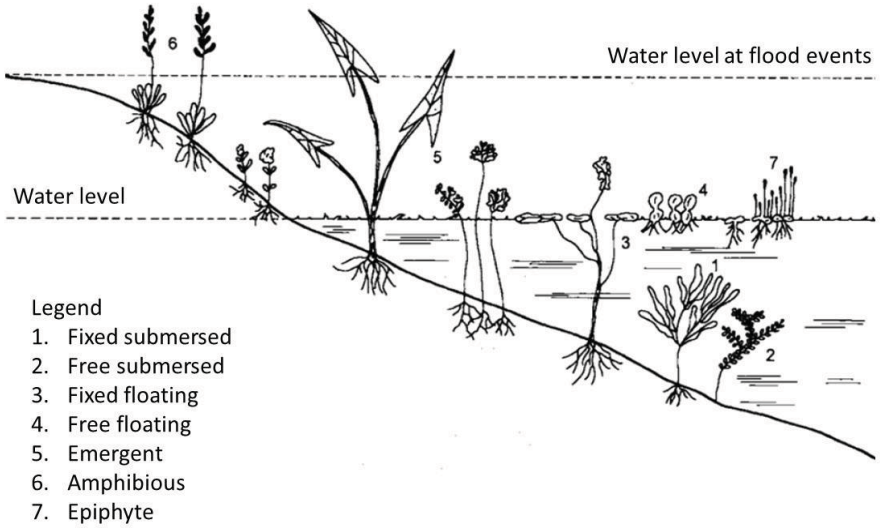

Figure 1. Life forms of aquatic macrophytes in accordance to Pedralli (1990).

Figura 1. Formas de vida de macrpofitas aquáticas de acordo com Pedralli (1990).

The diverse life forms of aquatic plants at the shoreline contribute to a complex structure of the littoral regions called riparian corridor (Lacerda *et al*., 2010). Given their complex biological structure, aquatic plants promote the association of high diversity of fishes, microscopic animals and algae, making littoral areas the most diverse in aquatic ecosystems (Galvão *et al*., 2014).

More than making physical structures, aquatic plants reduce sediment and pollutants transfer from land to water; acting as real filters in land-water interface accumulating and accelerating nutrients cycling. Also, they support the aquatic food chains. Aquatic plants are either directly being consumed by herbivores (Pompêo & Moschini-Carlos, 2003) or promote the growth of attached microscopic organisms that are consumed (Wetzel, 1981). Given all the above mentioned features, aquatic plants are usually nurseries and feeding areas for both fish and invertebrates (Thomaz *et al*., 2004).

Then, it is clear that aquatic plants are central to sustain biodiverse environments. The term "Biodiversity" refers to the variety of all life organisms in all their forms and interactions, comprising since genetic information

As diversas formas de vida de plantas aquáticas nas margens contribuem para uma estrutura complexa em regiões de margem denominada de corredor ripário (Lacerda *et al*., 2010). Em virtude dessa estrutura complexa biológica, plantas aquáticas promovem a associação de uma alta diversidade de peixes, animais microscópicos e algas, tornando essas áreas de margem as mais diversas nos ambientes (Galvão *et al*., 2014).

Mais do que proporcionar uma estrutura física, plantas aquáticas reduzem a transferência de sedimentos e poluentes das encostas para dentro dos corpos d'água; atuando como verdadeiros filtros na interface terra-água acumulando e acelerando a ciclagem de nutrientes. Além disso, elas suportam as cadeias alimentares. Plantas aquáticas são tanto diretamente consumidas por herbívoros (Pompêo & Moschini-Carlos, 2003) ou, promovem o crescimento de micro-organismos que são consumidos (Wetzel, 1981). Dito todas as características acima mencionadas, plantas aquáticas são usualmente berçários e áreas de alimento para peixes e invertebrados (Thomaz *et al*., 2004).

Logo, é nítido que plantas aquáticas são centrais para sustentar ambientes biodiverso; O termo "Biodiversidade"

until entire ecosystems (Hawksworth, 1995; Carrington, 2018). Biological diversity can be higher or lower depending on numerous aspects. Identifying the most important aspects that promote biodiversity has been a central goal in ecological researches. For instance, biodiversity is time-dependent considering organisms' dispersion and colonization in the habitats, and also considering the evolutive processes in which species evolve to use the environment differently in order to live together (the so called "niche differentiation") (Schluter, 2001). Environmental features of ecosystems, such as the productivity potential and the level of disturbances, can also explain differences among locations or over time in biodiversity (Myers *et al*., 2000).

Indeed, researches usually use sensible approaches that translate the role of conditions in which communities were submitted in biodiversity measurements. Precisely, species composition and richness (which and how many species occur in a location, respectively) were for a long time very used as the most important biodiversity measurements (Hawksworth, 1995).

Only species identity, however, may not have an efficient explanatory strength of biodiversity since species may

refere-se à variedade de organismos vivos em todas as suas formas e interações compreendendo desde a informação genética até ecossistemas inteiros (Hawksworth, 1995; Carrington, 2018). A diversidade biológica pode ser tanto alta quanto baixa dependendo de inúmeros aspectos. Identificar os aspectos mais importantes que promovem a biodiversidade tem sido um objetivo central entre pesquisadores ecólogos. Por exemplo, a biodiversidade é dependente do tempo considerando a dispersão de organismos e a colonização de habitats, e também considerando os processos evolutivos em quais espécies evoluem para usar os ambientes de forma diferente ao ponto de viverem juntas (conhecida por "diferenciação de nicho") (Schluter, 2001). Características ambientais dos ecossistemas tais como o potencial de produtividade e os níveis de distúrbios podem também explicar diferenças de biodiversidade entre localidades ou ao longo do tempo (Myers *et al*., 2000).

De fato, os pesquisadores usualmente usam abordagens sensíveis que traduzem a importância das condições em quais comunidades foram submetidas a medidas de biodiversidade. Precisamente, a composição de espécies e a riqueza (quais e quantas espécies em uma localidade, respectivamente) foram por

have similar or different life forms, as explained for aquatic plants. Then, ecosystem dynamics may be better understood if researchers measure the functional characteristics of organisms as an indicator of biodiversity (Cianciaruso *et al.*, 2009).

Functional biodiversity can be measured by estimating the range and value of characteristics that reveal the organisms' functional role in ecosystems (also known as functional traits) (Flynn *et al*., 2011). It is important to reinforce that the term "functional" refers to how does it work and not what it serves for. In this sense, the relation between biodiversity, ecosystem functioning and environmental restrictions is better comprehended by studying functional biodiversity (Mouchet *et al*., 2010). Recognizing and considering that species present distinct abilities and ecological functions, allow us to a greater or trustworthy explanatory strength of ecological functionality (Flynn *et al*. 2011).

Another face of biodiversity is the so called "phylogenetic diversity". This term refers to the diversity of organisms not considering their functional traits, but considering their relatedness after evolutionary processes. By many, phylogenetic diversity has been considered an important tool for

anos as medidas mais importantes para medir a biodiversidade (Hawksworth, 1995).

Entretanto, somente a identidade das espécies podem não ter um poder explicativo eficiente acerca da biodiversidade visto que as espécies podem ter formas de vida similares ou diferentes como explicado para plantas aquáticas. Assim, as dinâmicas de ecossistemas podem ser mais bem interpretadas se os pesquisadores medirem características funcionais dos organismos como um indicador de biodiversidade (Cianciaruso *et al*., 2009).

Diversidade funcional pode ser mensurada estimando a amplitude e valor das características que revelam a importância da funcionalidade dos organismos nos ecossistemas (também conhecidos como traços funcionais) (Flynn *et al*., 2011). É importante reforçar que o termo "funcional" se refere a como funciona e não para que serve. Dessa forma, a relação entre biodiversidade, funcionamento do ecossistema e restrições ambientais é mais bem compreendida por meio de estudos de diversidade funcional (Mouchet *et al*., 2010). Reconhecer e considerar que as espécies apresentam distintas habilidades e funções ecológicas nos permite um poder explicativo maior e/ou fidedigno da realidade do

biodiversity estimation (Clarke & Warwick, 1998; Faith, 2015). Overall, phylogenetic diversity tries to measure the amount of the evolutionary history of a set of species in a community (Faith, 1992; Forest *et al*., 2007; Winter *et al*., 2013). For that, as a family tree, species can be related in phylogenetic trees, in which much related species are link to few branches. Given that closely related species have a high change to be similar, functional traits among them may also be similar (Harvey & Pagel, 1991; Freckleton *et al*., 2002; Ackerly, 2009). If we have reliable phylogenetic trees, the phylogenetic diversity of a community can be easily estimated as the amount of branches linking all species of this community.

In a scientific work made by us, we studied functional and phylogenetic diversity of aquatic plants in a Neotropical floodplain located in South Brazil. We were able to find interesting novelties that help to understand how biodiversity relates to ecosystem dynamics.

The Neotropical floodplain studied is called the "Upper Paraná River Floodplain". It is a very important area for biodiversity conservation (Agostinho *et al.*, 2005) and have numerous aquatic habitats highly colonized by aquatic

funcionamento ecológico (Flynn *et al*. 2011).

Outra face da biodiversidade é a diversidade filogenética. Esse termo se refere à diversidade de organismos não considerando seus traços funcionais, mas sim seu parentesco após processos evolutivos. Logo, a diversidade filogenética tem sido considerada uma importante ferramenta para a estimativa da biodiversidade (Clarke & Warwick, 1998; Faith, 2015). Além disso, a diversidade filogenética procura medir a quantidade de história evolutiva de um grupo de espécies em uma comunidade (Faith, 1992; Forest *et al*., 2007; Winter *et al*., 2013). Para isso, assim como uma árvore genealógica, as espécies podem ser relacionadas em árvores filogenéticas nas quais, as espécies muito relacionadas estão ligadas por poucos galhos. Visto que espécies aparentadas possuem grandes chances de serem similares, os traços funcionais entre elas podem também ser similares (Harvey & Pagel, 1991; Freckleton *et al*., 2002; Ackerly, 2009). Se tivermos árvores filogenéticas fidedignas, a diversidade filogenética de uma comunidade pode ser facilmente estimada como a quantidade de galhos que abrangem todas as espécies dessa comunidade.

Em um trabalho científico feito por nós, estudamos a diversidade funcional e

plants (Thomaz *et al.*, 2009). After numerous studies, the habitats in the floodplain can be divided to three areas (the so called "subsystems") that are very distinct considering many environmental aspects and also considering the species that inhabit (see evidences in Roberto *et al.*, 2009; Padial *et al.*, 2012). Even so, after studying the functional features of aquatic plants, we found that species that differ among subsystems play a redundant role considering their functional features. There is only weak evidence that species that colonize subsystems may have distinct aspects considering their life forms. Our results, although novel, are well supported by classical ecological theory. In accordance to Walker (1992), most species in an ecosystem are redundant in regard to environmental functionality, and few are important for most ecosystem maintenance. In this case, species could be compared to all persons in an airplane, which functionality depends mostly on the crew. However as species are being loss or removed, the redundancy decreases and, any further changes could reverberate in ecosystem functionality loss. Surely, the analogy is not full correct given that redundant species could substitute the "important" species in case of losses. Given that the

filogenética de plantas aquáticas de uma planície de inundação Neotropical localizada no Sul do Brasil. Fomos capazes de encontrar novidades interessantes que nos auxiliaram a entender como que a biodiversidade esta relacionada com as dinâmicas ecossistêmicas.

A planície Neotropical estudada é denominada de Planície de Inundação do Alto Rio Paraná. É uma área muito importante para a conservação da biodiversidade (Agostinho *et al*., 2005) e possui muitos habitats aquáticos altamente colonizados por plantas aquáticas (Thomaz *et al*., 2009). Após inúmeros estudos, os habitats da planície podem ser divididos em três áreas (conhecidas por subsistemas) que são muito diferentes considerando muitos aspectos ambientais assim como as espécies que neles habitam (veja evidências em Roberto *et al.*, 2009; Padial *et al.*, 2012). Mesmo assim, após estudar características funcionais de plantas aquáticas, descobrimos que as espécies que diferem entre subsistemas são redundantes considerando suas características funcionais. Existe apenas uma fraca evidência de que as espécies que colonizam os subsistemas podem ter aspectos distintos em relação às suas formas de vida. Nossos resultados, embora inéditos, são suportados por teoria ecológica clássica. De acordo com Walker

subsystems of floodplains are composed by redundant species (even if they are not the same among subsystems), we may conclude that the functional diversity of aquatic plants sustain the ecosystem functioning: many redundant species provide greater guarantees that some will maintain functioning even if others fail (Yachi & Loreau, 1999).

Likewise, we also develop evidence that functional diversity changes over time and space taking in response to different ecological predictors. The change was with several peaks. Depending on the scale, we generated evidence that nutrient and floods may promote the functional diversity. But the most important result is that most indexes of functional diversity are decreasing over time, even with the fact that more species are being identified, mostly because researchers are becoming more experts in species identification. Then, we can suggest that there is a scenario of functional homogenization of the aquatic plants. However, such homogenization can be explained by the fact that the more species identified recently by trained researchers are probably functional redundant. Even so, our results also reinforce the role of long term ecological studies to the understanding and

(1992), muitas espécies em um ecossistema são redundantes quanto à funcionalidade ambiental e poucas são importantes para a manutenção do ecossistema. Nesse caso, as espécies podem ser comparadas com todas as pessoas em um avião, onde a funcionalidade depende principalmente da tripulação. Contudo, à medida que as espécies são perdidas ou removidas, a redundância diminui e, qualquer alteração futura pode resultar em perda da funcionalidade ecossistêmica. Logicamente que a analogia não é inteiramente correta visto que espécies redundantes podem substituir espécies "importantes" em caso de perdas. Visto que os subsistemas são constituídos por espécies redundantes (mesmo que não no mesmo ecossistema), podemos concluir que a diversidade funcional de plantas aquáticas sustenta o funcionamento do ecossistema: muitas espécies redundantes permitem uma maior garantia de que o funcionamento será mantido mesmo que as demais venham a falhar (Yachi & Loreau, 1999).

Da mesma forma, nós desenvolvemos evidências de que a diversidade funcional se altera ao longo do tempo e do espaço considerando diferentes preditores ambientais. Mas o resultado mais importante é de que muitos índices de diversidade funcional estão diminuindo ao

management of functional diversity.

Lastly, we also analyzed phylogenetic diversity at the Neotropical floodplain along time and at different spatial scales: considering all floodplain, only subsystems, and individual lakes as a unit for analysis. In general, we have shown that aquatic plants are structured considering their relatedness and environmental conditions depending on the scale. As already mentioned, the three subsystems are largely known as different aquatic environments. In agreement, phylogenetic relatedness is dependent on subsystems, what indicate that subsystems also differ in their evolutionary development of species. Indeed, species selection most likely occurs due to particularly environmental conditions and evolutionary processes present uniquely at each subsystem. In this case, differences in nutrient concentrations are evident. Therefore species selection also causes selection of different biological lineages of the phylogenetic tree; which was also related to the life forms of aquatic plants.

Taking into account all of the novelties found by us, we believe that functional and phylogenetic diversity studies clarify many ecological questions concerning aquatic plants. Plants have a great role at aquatic environments, and

longo do tempo, mesmo com o fato de que muitas espécies estão sendo identificadas, principalmente porque os pesquisadores estão se especializando mais na identificação das espécies. Logo, podemos sugerir que existe um cenário de homogeneização funcional de plantas aquáticas. Entretanto, tal homogeneização pode ser mais bem explicada pelo fato de que mais espécies identificadas recentemente por pesquisadores aptos são provavelmente redundantes funcionalmente. Mesmo assim, nossos resultados reforçam a importância de estudos ecológicos de longo prazo no entendimento e manutenção da diversidade funcional.

Por fim, também analisamos a diversidade filogenética na planície Neotropical ao longo do tempo e em diferentes escalas espaciais: considerando toda a planície, apenas subsistemas e lagoas individuais como unidades de análise. Em geral, mostramos que plantas aquáticas são estruturadas considerando seu grau de parentesco e condições ambientais as quais estão sujeitas de acordo com a escala espacial. Como já mencionado, os três subsistemas são muito conhecidos por serem diferentes entre si quanto aos seus ambientes aquáticos. De acordo, o parentesco filogenético é dependente do subsistema, o que indica

our study was relevant to fill several knowledge gaps in the ecology of aquatic plants. As a major conclusion, we recognize that aquatic plants communities indeed could present many distributional patterns along environmental gradients. However such patterns are likely context dependent and poorly previewed.

que os subsistemas também diferem no desenvolvimento evolutivo das espécies. De fato, a seleção das espécies ocorre principalmente em virtude de condições ambientais e processos evolutivos típicos de cada subsistema. Dessa forma, a seleção das espécies também causa uma seleção nas linhagens biológicas da árvore filogenética; o que também se relacionou com as formas de vida das plantas aquáticas.

Tomando em conta todas as novidades encontradas em nossas pesquisas, acreditamos que os estudos com diversidade funcional e filogenética esclarecem muitas perguntas ecológicas que envolvem plantas aquáticas. Plantas apresentam uma importância essencial nos ambientes aquáticos, e nosso estudo foi relevante para preencher diversas lacunas do conhecimento referente à ecologia de plantas aquáticas.

Como uma conclusão geral, reconhecemos que as comunidades de plantas aquáticas, de fato apresentam diversos padrões de distribuição ao longo de gradientes ambientais. Entretanto, tais padrões são dependentes do contexto em questão e pouco previsíveis.

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CHAPTER 1

ENVIRONMENTAL AND TAXONOMIC HETEROGENEITY DOES NOT GUARANTEE FUNCTIONAL COMPOSITION DISSIMILARITY FOR AQUATIC MACROPHYTES COMMUNITIES

Environmental and taxonomic heterogeneity does not guarantee functional composition dissimilarity for aquatic macrophytes communities

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Abstract

Differences in ecological communities are described by their species similarity or distinctness. Taking into account the community composition at a determined site, one could expect a similar reasoning explaining both taxonomic and functional composition differences due to environmental gradients. We aim to evaluate spatial variation in functional composition of aquatic macrophyte assemblages in a Neotropical floodplain. This floodplain is well characterized by encompassing different subsystems considering both environmental features and taxonomic composition differences. We therefore hypothesized that functional composition also differs among subsystems. Contrarily to what we expected, there were poor functional composition differences among the subsystems. There is only little evidence that some life forms are more or less observed in certain subsystems. It is interesting that the considerable environmental heterogeneity is reflected only in taxonomic, but not in functional composition. The explanation for this result is that different species have high functional redundancy: different functional traits could be recorded at all subsystems. Therefore, we suggest that the whole ecosystem functioning is probably insured by species functional redundancy at the Neotropical floodplain. However, we can never rule out the fact that the choice of traits could effect interpretations, and the selection of traits should be better explored, particularly for aquatic macrophytes.

Keywords

Community structure; Environmental filtering; Functional traits; Homogenization.

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Introduction

Two ecological processes majory reported as possible responsible for structuring communities are limiting similarity and environmental filters (Pausa and Verdú 2010), particularly in a scale with few dispersal limitation (Vellend 2010). Limiting similarity considers that species co-occur at determined sites due to functional traits distinction. Therefore, resources exploration is different among species, resulting in low niche overlap (Tilman 2001; Pocheville 2015). If low, niche overlap usually ensures species co-occurrence (Diamond 1975; Cazelles et al. 2016). If high, niche overlap means a common use of resources, resulting in local species competitive exclusion when resources are limited (Pocheville 2015) even through small niche differences have been reported as sufficient for species coexistence (Chesson, 2000). Environmental filtering, in turn, is known as the effect of environmental factors selecting species; allowing their establishment, survival, reproduction and persistence in a suitable site (Heino et al. 2015). In a set of environmentally different ecoregions, filters may cause dissimilarity in both taxonomic and functional composition (Lamarre et al. 2016). On the other hand, if environmental filters are transposed (particularly in groups of high environmental plasticity), species may exhibit high functional similarity enabling niche overlap and resource competition (Funk et al. 2008; Weiher et al. 2011) decreasing species relative abundances and promoting competitive exclusion (Garrett 1960; Tilman 2001). Therefore, taxonomic compositional differences are not always related to functional compositional dissimilarities.

The environmental filtering is common mainly when the environmental gradient is strong and do result in species pool selection, causing metacommunities local differences (Pillar et al. 2009). More than taxonomic differences, trait-based community assembly patterns along environmental gradients also allow the explanation of functional differences at different scales (Pillar et al. 2009) and may contribute in creating more quantitative and predictive community ecology (McGill et al. 2006). One may expect that if taxonomic composition differs in response to environmental filtering, functional composition may also differ (Lamarre et al. 2016). On the other hand, taxonomic differences may be generated by dynamic processes of colonization and competitive exclusion of functionally similar species; and the taxonomic differences are not

always reflected in differences of functional composition (Pavao-Zuckerman and Coleman 2007).

Previous studies have shown clear taxonomic differences related to "subsystems" that are defined as regions inside the floodplain with different environmental characteristics caused by the influence of different rivers (Padial et al. 2009; 2012). Subsystems in this floodplain differ especially considering limnological, geomorphological and biological features; which define the major ecological gradient (Roberto et al. 2009), that explain overall biodiversity (Santos and Thomaz 2007; Thomaz et al. 2009). Therefore, the overall suggestion is that environmental filtering related to subsystem is strong in the floodplain, causing community assembly (Thomaz et al. 2009, Padial et al. 2012). However, evidences above are limited to taxonomic composition. Particularly for aquatic macrophytes dynamics, their response to ecological filters has been usually understood through the use of functional traits in (Shipley et al. 2011).

Environmental filtering in functional composition of aquatic macrophytes have strong implications for ecosystem functioning, given the role of aquatic macrophytes in structuring aquatic ecosystems, affecting diversity and ecological relations (Jeppensen et al. 1998; Meerhoff et al. 2003; Cunha et al. 2011). Relatedly, Tilman et al. (1997) highlighted that understanding variations in functional composition are essential for knowledge of ecosystems processes (see also Cadotte et al. 2011). Here, we aimed to test the hypothesis that functional composition of aquatic macrophytes communities differ among subsystems of a Neotropical floodplain, following a clear taxonomic difference. We used functional metrics to describe the variation in functional composition of aquatic macrophytes assemblages over 15 sampling sites in the Upper Paraná River floodplain. As a consequence, environmental filtering may also affect 'ecosystem functionality' of the floodplain, mainly considering the well-recognized functional role of aquatic macrophytes (Pandit 1984).

Material and methods

The study was conducted in the Upper Paraná River floodplain (UPRF), South Brazil (53º00'W; 53º40'W; 22º30'S; 23º00'S) (Agostinho and Zalewski 1996). The intense record of aquatic macrophytes communities (Thomaz et al. 2002; Ferreira et al. 2011; Souza et al. 2017) reinforce the fact that the UPRF is an important biodiversity hotspot for aquatic communities (Ferreira et al. 2011). Environmental differences of three hydrological subsystems are considered the major environmental gradient in the UPRF. Such subsystems (named as "Paraná", "Baia" and "Ivinhema") are characterized by a main river channel and several associated lakes. Subsystems differ from each other giving their distinct geomorphological origins and features (source of organic matter, water flow, limnological variables, etc.) (Roberto et al. 2009).

We have sampled aquatic macrophytes, following Pedralli et al. (1990) classification, from five different lakes of each of the three subsystems of the UPRF in November of 2015. Species were collected along the entire shoreline of all lakes and maintained moisture in 100 L plastic bags until correct identification and trait measurements. The sampling methodology followed Pérez-Harguindeguy et al. (2013), which proposed a module sampling for vegetative propagation species. A module can be described as the simplest minor repeating portion containing root, stem and leaves. This methodology was established giving the intense vegetative propagation of aquatic macrophytes species, making the identification of an individual very difficult. For each module, we chose 17 functional traits (Table 1) in order to access aquatic macrophytes functional composition: 10 traits were directly measured in modules, and seven (7) traits were defined for each species according to specialized literature. See details and justification of chosen traits in Supplementary Material 1.

Traits related to morphology, growth and life form have been commonly used to describe how environmental conditions (Ali et al. 1999; Griffin-Nolan et al 2018) affect the reproduction, grow and species survival (Cavalli et al. 2014). Unfortunately, we were unable to use physiologic traits due to uncommon use, high costs and difficulty in estimations (Zhang 2004). However, we believe that, at least for our main goal, the chosen traits fulfill the mission

in describing functional composition among different subsystems given the fact that many functional traits translate importante physiologic aspects (leaves morphologic aspects are linked to photosynthesis).

Table 1. List of functional traits chosen to describe aquatic macrophytes functional composition, indicating traits obtained from literature information, or directly measured after field sampling.

	CLASSIFICATION	TRAITS
OBTAINED FROM LITERATURE	Plant	*Amphibious*
		Emergent
		Epiphyte
		Fixed floating
		Free floating
		Fixed Submerged
		Free Submerged
		Annual
		Perennial
		Monthly blooming
		Semester blooming
		Annual blooming
	Leaf	*Glabrous pilosity*
		Pilous pilosity
		Coriaceous consistency
		Herbaceous consistency
	Stem	*Erect*
		Prostrate
	Root	*Fasciculate*
		Pivoting
MEASURED IN THE LABORATORY	Plant	*Height (cm)*
	Leaf	*Width (cm)*
		Length (cm)
		Thickness (mm)
	Petiole	*Length (mm)*
		Presence/ absence
	Stem	*Thickness (mm)*
		Presence/ absence
	Root	*Length (cm)*
		Presence/ absence

The function composition of the aquatic macrophytes communities was measured by the community-level weighted means of trait values (CWM) (Lavorel et al. 2008). In this case, matrices of species presence/absence per subsystem and, species per traits were created for all 15 lakes (five from each subsystem). A Principal Coordinate Analysis (PCoA) was used to visualize patterns in functional composition. We formally tested for differences in functional composition among subsystems using a Permanova (Anderson et al. 2001). The same analyses above were made for presence/absence taxonomic composition, which was made only to clearly demonstrate differences among subsystems, as anticipated (see results). To characterize typical species per subsystems, we then used an indicator value analysis (IndVal - Dufrêne and Legendre 1997). Species with high IndVal values indicate species that i) occurs mostly in one subsystem and ii) in most sampling lakes of such subsystem (the "specificity" and "fidelity" facets of IndVal, respectively; Dufrêne and Legendre 1997). For all analyses above, we used the following functions and packages in R environment (R Core Team 2018): function 'functicomp' for functional composition in the "FD" package (Laliberté et al. 2015), functions 'pco' for PCoA and 'indval' for IndVal in "labdsv" package (Roberts 2016), and functions 'vegdist' for distance matrices and 'adonis' for Permanova in "vegan" package (Oksanen et al. 2017).

Results

46 species of aquatic macrophytes were recorded in the fifteen sampled lakes of the UPRF. Considering the five modules per species and the 10 measured traits, a total of 1,610 continuous traits were measured. As anticipated, the three subsystems (Paraná, Baia and Ivinhema) clearly differ from each other considering taxonomic biodiversity (Permanova: $F=3.28$, $R^2=0.35$, $P=0.001$) (Figure 1a). According to the IndVal, Paraná subsystem had *Ludwigia peruviana* as an indicator species (IndVal=1, $P=0.001$) occurring in the five lakes sampled. *Limnobium laevigatum* was an indicator species of Baia subsystem (IndVal=0.8, $P=0.01$) occurring in four of the five lakes sampled. Ivinhema subsystem had no indicator species.

On the other hand, functional composition did not significantly differ among subsystems (F=1.41, R^2=0.19, *P*=0.238) (Figure 1b). The only patterns that can be suggested considering the PCoA, albeit weak, are: i) emergent life form species seems to be typical in nearly all lakes of the Paraná subsystem (Figure 1b) and ii) fasciculate roots were mostly observed in lakes from Baia and Ivinhema subsystems (Figure 1b).

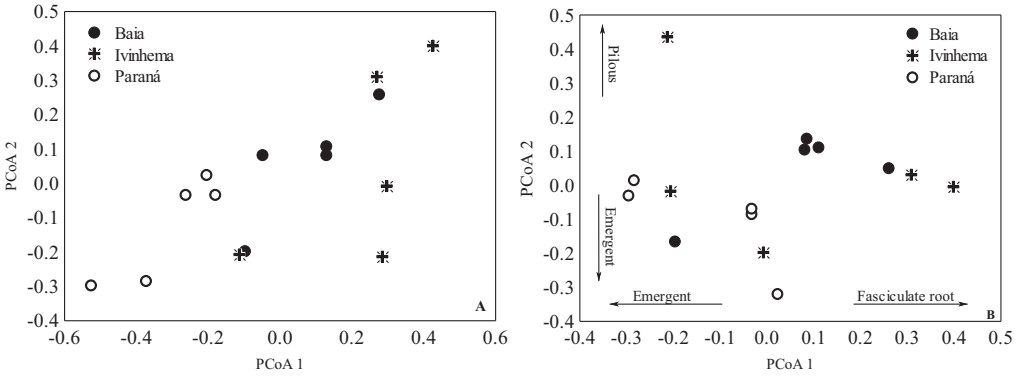

Figure 1. Principal Coordinate Ordination Analyze (PCoA) from the aquatic macrophytes of the three subsystems of the UPRF considering a) taxonomic diversity (presence/absence) and; b) functional composition.

Discussion

In this study, we have tested if spatial variation of the aquatic macrophytes functional composition responds to environmental classification considering three different subsystems in a Neotropical floodplain. Contrarily to the observed for taxonomic composition, there is poor functional composition differentiation among the ecological heterogeneous subsystems. Environmental heterogeneity has long since been described as species richness and biodiversity predictor (Yang et al. 2015; Bergholz et al. 2017; Pinha et al. 2017). Heterogeneous sites promote species sorting, resulting in beta diversity among local communities of a metacommunity (Pinha et al. 2017). This was already demonstrated in the UPRF for several biological groups, ranging from microscopic algae to fish (Padial et al. 2012).

It has also been shown that environmental filtering can shape functional composition at different environmental sites, as a result of differential species recruitment and establishment (Fortunel et al. 2014). Therefore, it is interesting that the considerable environmental

heterogeneity is reflected only in taxonomic, but not in functional composition. Probably, functional composition can be related to other local peculiarities and characteristics unrelated to environmental classification in subsystems. We initially expected that environmental filtering promoted by subsystems could select species with similar functional features within a subsystem, and different functional features between subsystems. Our results show the opposite: a 'functional homogenization' among subsystems, indicating that the different species from subsystems are functionally redundant (see also Kang et al. 2015). Therefore, the most likely explanation for our results may be related to low co-existence of functionally similar species within a subsystem, as expected in limiting similarity theory (Abrams 1983). As a consequence, functionally similar species are observed among, and not within, subsystems. Surely, an interaction of deterministic and stochastic factors affect community structure between and within subsystems (see also Padial et al. 2014), but our results at least suggest that the known taxonomic differences among subsystems may be a result of poor co-existence of similar species.

We must highlight that our results do not necessarily indicate that the functional homogenization among subsystems is a result of a decline in specialist species (as suggested by Clavel et al. 2011), which could have consequences to ecosystems functioning and productivity. Only long-term studies reporting a decline in functional diversity indexes could state that functional homogenization is a concern of ecosystem functioning. Also, the fact that subsystem classification was a poor predictor of functional composition does not mean that environmental filtering is unimportant to explain differences of functional traits or ecosystem functioning (Karadimou et al. 2016).

Here, we investigated traits that usually respond to environmental variation, as those related to life form, roots and leaves. For instance, i) emergent species are usually the most abundant (Thomaz et al. 2002; Alves-da-Silva et al. 2014) occurring in shallow belts and along the riverside (Pott et al. 1989); ii) submerged species occur when transparency is high (Bornette and Puijalon 2011); iii) free-floating species are abundant in high nutrient concentration in water column (Bornette and Puijalon 2011); iv) fasciculate roots for aquatic macrophytes

develop an important role guarantying air reserve (allowing floating) and nutrient rapid achievement (e.g. nutrient assimilation area extended throughout the water column by root nutrient quest considering floating species for example) (Tabata et al., 2015; Pereto et al., 2016); v) the presence of trichomes on leaf blade could be efficient as a mechanical barrier against herbivores and/or pathogens (Werker, 2000) and guarantee a micro climate around the stomata avoiding water loss (Buckley 2005); and so on. At least for the scale observed in our study, even a strong environmental gradient (see Roberto et al. 2009) was not enough to promote functional differences. Maybe, differences could be observed in other scales, or considering other dimensions (e.g. temporal differences related to the well-known hydrological regime of floodplains).

Still, the lack in functional composition differentiation could also be explained by traits considered. We can never rule out that the choice of traits may affect interpretations (Zhu et al. 2017). Indeed, aquatic macrophytes have an extreme plasticity in morphological measurements (Li et al. 2016), and this ensure ecosystem functioning when community is composed by species with different traits (Jackrel and Morton 2018). Therefore, some coarse (but classical) classifications may be more meagninful to consider the similarity in plant functions and response to environmental gradients, such as the life form classification (see also Schneider et al. 2018).

On the other had, some authors argue that more details in traits are necessary to understand aquatic macrophyte responses to environment (Gratani 2014). For instance, Steffens and Rasmussen (2016) highlight the possible relevance in considering not only adventitious (or fasciculate) root or not but classify it in types of adventitious roots (flood, nutrient or wound induced). In accordance to these authors, each type of adventitious roots is regulated and responds to the submitted environmental condition in different ways (Steffens and Rasmussen 2016). Taking into account the importance in choosing traits related to the ecological question to be answered (Diaz et al. 2013; Zhu et al. 2017; Griffin-Nolan et al 2018) and how the chosen traits can maximize ecosystem function (Cadotte 2017; Fu 2018), we encourage future studies to explore in details which traits should be used to test for different ecological hypotheses.

Functional traits biodiversity promote ecosystem functioning giving the capacity of species in exploiting resources at different spaces and time (Fetzer et al 2015; Gross et al. 2017). Here, we have shown that environmental filtering acting in taxonomic composition not always select different functional composition, indicating that ecological studies may encompass different facets of biodiversity for a better link between biodiversity and ecosystem functioning. Also, we conclude that the functional redundancy of species among subsystems may also promote insurance for whole ecosystem functioning of floodplain (Yachi and Loreau 1999).

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Supplementary Material 1 – Chosen functional traits justification

Life form - species classification according to Pedralli (1990). The life form indicates the strategy of habitat adaptation were between aquatic macrophytes, species range from amphibious to totally submerse (Irgang & Gastal Jr. 1996).

Persistence - species classification in order to be annuals or perennial. The persistence time reveal the contribution of the organism to the ecosystem function (Pérez-Harguindeguy et al., 2013).

Blooming duration - the blooming duration reveal a greater reproductive success beyond the fact that the organism influences the rounding environment offering resources to the local biota in terms of seeds, fruit and biomass function (Pérez-Harguindeguy et al., 2013).

Height (cm) - measure made from the base line of the shoot to the upper photosynthetic region. This height measure reveals vigor and light competition between organisms (Westoby et al., 2002; Pérez-Harguindeguy et al., 2013).

Leaf width (cm) - measure of the wider portion of an imaginary circle on the leaf blade. According to Pérez-Harguindeguy et al., (2013) this measure have been considered as much efficient as leaf area in a way that with a greater surface contact area, the greater the canopy dominance.

Leaf length (cm) - measure of the longest portion of the leaf blade. This trait is supplementary to leaf width reflecting de surface contact area to canopy dominance (Pérez-Harguindeguy et al., 2013).

Leaf thickness (mm) - mean leaf thickness in 5 different points of the leaf blade excepting the main vein. This trait provides informations about the investment in cuticle, palisade and spongy parenchyma as well species strategies for resource acquisition and use (Kitajima & Poorter 2010).

Petiole length (mm) - measure of the total petiole length. This trait helps the leaf blade in the capture of light for the photosynthetic activity. We believe that longer petioles would contribute to a greater light absorption and consequently to a greater photosynthetic activity considering that petiole length and leaf blade length are highly associated (Abrahamson 2007).

Pilosity - the presence of trichomes at the leaf blade guarantee a micro climate around the stomata avoiding water loss (Brewer, Smith & Vogelmann 1991). Trichomes can also be efficient as mechanical barriers against herbivores, pathogens and intense light (Werker 2000) as well as reducer of radiation absorption reducing transpiration (Skelton et al., 2012).

Leaf consistency (cm) - the leaf texture reflects an efficient water economy strategy. This trait is supplementary to pilosity. We believe that leafs with a more coriaceous texture are more efficient in water economy due to the presence of a thick cuticle (Pérez-Harguindeguy et al., 2013).

Stem - diagnosis of stem being prostrated or erect resulting in more or less shade for neighboring organisms as well as wind exposure. According to Henry & Thomas (2002) taller plants growth on the occurrence of shade and/or no wind, while shorter plants growth on sun and/or wind exposure.

Stem thickness (mm) - measure of the middle part of the role stem length with the help of a digital pachymeter. The stem thickness reveals the efficiency on aerenchyma investment for better gas diffusion inside the plant (Pérez-Harguindeguy et al., 2013).

Root length (cm) - measure of the longest root. The root length indicates the need for nutrients. In this sense, we believe that a longer root will reveal a plant poorly supplied with nutrients while a shorter root will reveal a plant well supplied by nutrients around (Tabata et al., 2014)

Root architecture - diagnosis about the root being pivoting or fasciculate. Root architecture has already been associated to water availability (Fitter et al., 1991).

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CHAPTER 2

EXPLAINING TEMPORAL PATTERNS OF AQUATIC MACROPHYTES FUNCTIONAL DIVERSITY IN A NEOTROPICAL FLOODPLAIN

Explaining temporal patterns of aquatic macrophyte functional diversity in a Neotropical floodplain

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Summary

Several ecological mechanisms explain functional diversity of ecological communities. The fluctuation of environmental predictors may thus be related to functional diversity. We explored effects of environmental heterogeneity, nutrient availability, alkalinity, and hydrological regime on long-term patterns of functional diversity in aquatic macrophyte communities inhabiting a Neotropical floodplain. We used functional diversity indexes estimated at different spatial scales in 38 sampling periods distributed over 11 years. Functional diversity indexes (FRic, FDis, FDiv and RaoQ), as well as functional beta diversity (BetaSIM and BetaSOR), representing inter-site functional diversity variation, were calculated for each sampling period considering aquatic macrophyte occurrences and measurements of specific functional traits. Traits were gathered from literature and estimated in a snapshot sampling of 5 modules for each of the 76 taxa recorded. A module was determined as the minor repeating portion containing a root, stem, and leaves. High and low peaks of functional diversity were coincident to variations in predictors, depending on the spatial scale considered. It can be ascertained that, along the 11 years, FRic index increased while the other indexes generally decreased regardless of the spatial scale considered. Probably, the increase in FRic could be ascribed to a known taxonomic identification bias in the Long-Term Ecological Program. Even with such a bias, the other functional indexes exhibit temporal homogenization. Functional redundancy among species could be attributed to such pattern with potential effects on ecosystem stability. We also generated evidence that functional diversity responds, at least in part, to the different ecological predictors.

Keywords: Aquatic ecosystems, functional redundancy, functional scale, functional traits, homogenization.

1. INTRODUCTION

Functional diversity (FD) has attracted the attention of ecologists for expressing how ecological communities and maintenance processes are related (Petchey & Gaston, 2006). It is known that ecosystem services (McGill, Enquist, Weiher & Westoby, 2006), which are central to human welfare (Vitousek, Mooney, Lubchenco & Melillo, 1997), contribute to ecosystem functioning and may be better explained by functional rather than taxonomic diversity. Indeed, FD is frequently associated with ecosystems processes (Fu et al., 2014). Environmental changes, number of species and invasions events can affect negatively FD (Cadotte, Carscadden & Mirotchnick, 2011). In this sense, studies that seek to explain FD have evaluated its temporal variation (Frainer, McKie & Malmqvist, 2014) along with the likely effects of environmental drivers.

In this regard, it has been suggested that temporal variation in ecosystem functioning is reflected in FD (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Villéger, Miranda, Hernandez & Mouillot, 2010). The first obvious expectation is that the increase in species richness could lead to an increase in FD (Burkepile & Hay, 2008; Jousset, Schmid, Scheu & Eisenhauer, 2011). However such a positive relationship (and thus a redundancy in representing biological diversity) may not always be true as the new species could have traits already present in the community (Joner, Specht, Müller & Pillar, 2011), the so-called functional redundancy (Kang et al., 2015). This reinforce the importance in not only measure species richness to explain biodiversity and implement conservation efforts (Cadotte, Carscadden & Mirotchnick, 2011)

Environmental heterogeneity is one of the major predictors responsible for biodiversity maintenance because it denotes dissimilarity between sites and so the niche spectrum for multiple micro-habitats (Simpson, 1949; Heino, Gronroos, Soininen, Virtanen & Muotka, 2012; Heino, Melo & Bini, 2015). It is thus suggested that a heterogeneous environment, and hence a more biodiverse one (Leibold et al., 2004),

contributes more effectively to ecosystem functioning (Cardinale et al., 2011) than a homogeneous and less biodiverse environment (Tilman, 2001; Thomaz, Bini & Bozelli, 2007). Relatedly, heterogeneous sites promote species composition variation (Heino, Gronroos, Soininen, Virtanen & Muotka, 2012; Heino, Melo & Bini, 2015; Boschilia, Oliveira & Schwarzbold, 2016; Alahuhta et al., 2017). Therefore, a strong relationship between environmental heterogeneity and FD in aquatic habitats is assumed (Palmer & Poff, 1997).

Another common predictor of biodiversity is nutrient availability, which is reflected in primary productivity (Tilman, 2001). A positive relationship between biodiversity and nutrient availability is expected since, in more productive ecosystems, there is more energy to support complex food webs (Tilman, Lehman & Thomson, 1997; Tilman, 2001). However, beta diversity may have a positive, negative or hump-shaped relationship with productivity depending on the spatial scale adopted (Chase & Leibold, 2002). Even so, few studies (Roscher et al., 2013; Chanteloup & Bonis, 2013; Jänes et al., 2016) have focused on the effects of nutrient availability on community's FD.

In aquatic habitats, other predictors of FD have been proposed. For instance, alkalinity is well known as an important water chemistry variable influenced by the surface and underlying geology affecting aquatic macrophytes distribution in most regions of the world (Kissoon et al., 2013; Heegaard, Birks, Gibson, Smith & Wolfe-Murphy, 2001). It is a measurement of carbonates, bicarbonates and hydroxides that is, all dissolved alkaline substances in water (Tailling, 2010).

In floodplains, hydrologic regimes play a key ecological role by structuring biodiversity patterns and guiding ecosystem functioning (Junk, Bayley & Sparks, 1989), especially to estimate biodiversity (Bady et al., 2005). It is known that flood events

result in homogenization of aquatic systems, turning different sites ecologically similar (Thomaz, Bini & Bozelli, 2007) and decreasing taxonomic beta-diversity (Bozelli, Thomaz, Padial, Lopes, & Bini, 2015; Ceschin, Bini & Padial, 2018). Contrarily to taxonomic beta-diversity, extreme flooding events associated with heterogeneous patterns of water flow may promote FD (Lawson, Fryirs, Lenz & Leishman, 2015). As an example, low hydrologic levels at riparian communities may cause stress and constrain functional dispersion; however, the hydrologic levels increase contribute to niche space enlargement favoring different ecological strategies of opportunistic species (Lawson, Fryirs, Lenz & Leishman, 2015).

Even considering the abovementioned relationships, it remains poorly understood which predictors contribute to FD variation in several aquatic communities using long-term data. This is true for aquatic macrophytes in temporal dynamic ecosystems such as floodplains. Aquatic macrophytes play a central role in floodplains, affecting the biodiversity and ecological relationships of other aquatic communities (Jeppesen, Lauridsen, Kairesalo & Perrow, 1998; Meerhoff, Mazzeo, Moss & Rodríguez-Gallego, 2003; Cunha et al., 2011). The objective of this study was to describe and explain FD variation in aquatic macrophyte communities over 11 years in a Neotropical floodplain. We hypothesized that FD would not monotonically increase or decrease over time, but vary according to predictors of flood pulse, environmental heterogeneity, and productivity which have been related to taxonomic beta-diversity (Soares et al., 2015; Ceschin, Bini & Padial, 2018). Six floodplain lakes (two lakes from three different subsystems) were sampled on a quarterly basis, and temporal variation was explained regarding 38 sampling periods in both floodplain-FD and subsystem-FD (i.e., inter-site functional variation). The scale of analysis was also changed by explaining FD for each of three main subsystems within the Neotropical floodplain. This change is due to the

fact that the subsystems in this floodplain have been shown to differ in terms of biotic and abiotic features (Padial et al., 2012). As a consequence, we hypothesized that FD predictors would differ for each subsystem, and possibly become more apparent in finer scales (Pasari, Levia, Zavaleta & Tilman, 2013).

2. METHODS

Study area

The Upper Paraná River Floodplain (UPRF) is located in the northeastern Paraná State in Southern Brazil (53º00'W; 53º40'W; 22º30'S; 23º00'S) (Agostinho & Zalewski, 1996), and it is considered a biodiversity hotspot of aquatic macrophyte communities (Ferreira, Mormul, Thomaz, Pott & Pott, 2011). The main source of environmental variation in the UPRF is related to three different subsystems characterized by three main rivers (Baia, Paraná, and Ivinhema Rivers) that differ in their limnological, biological and geomorphological features (Roberto, Santana & Thomaz, 2009; Padial et al., 2012). Specifically, the Paraná River (PR) is characterized by frequent flood pulses though with low amplitude; low nutrients inputs; and high water flow and transparency. The Ivinhema River (IV), in turn, has intermediate water flow, high water turbidity, and high phosphorus concentrations. Lastly, the Baia River (BA) has high nutrient inputs, especially nitrate and dissolved carbon concentrations, due to the presence of humic compounds and low water flow (Roberto, Santana & Thomaz, 2009).

Drought and flood periods affect this floodplain as well as all the subsystems abovementioned. Nonetheless, the duration and intensity of floods have been affected by dam operations downstream and upstream Paraná River (Agostinho, Thomaz, Minte-Vera & Winemiller, 2000). Still flood pulses remain the main driving force of aquatic

macrophyte communities in the UPRF (Thomaz, Carvalho, Padial & Kobayashi, 2009). During floods, lakes become more connected and similar in terms of environmental features and communities due to increased dispersal. Conversely, during droughts, environmental dissimilarities are enhanced due to lake isolation and local conditions, which contribute to distinct communities as a consequence of species sorting and dispersal limitation (Thomaz, Bini & Bozelli, 2007; Padial et al., 2014).

Dataset and functional traits

A dataset of aquatic macrophyte occurrence sampled in a Long-Term Ecological Project conducted in the UPRF from 2002 to 2012 was used. The database comprises quarterly samples (February, May, August and November) totaling 38 sampling periods (Dittrich, Dias, Bonecker, Lansac-Tôha & Padial, 2016; Ceschin, Bini & Padial, 2018). In general, the period from December to May is characterized by higher water levels; while the period from June to November is considered a drought period, although some flooding episodes have been recorded (Dittrich, Dias, Bonecker, Lansac-Tôha & Padial, 2016). Samples were collected from six permanent lakes, two in each of the UPRF subsystem. All aquatic macrophytes taxa recorded in the Long-Term Ecological Project were checked and classified according to Pedralli (1990). In total, 76 taxa were considered since some were identified only at a genus level (Supplementary Material 1).

Unfortunately, the Long-Term Ecological Project did not consider measurements of aquatic macrophyte attributes. The main goal was to explore and analyze taxonomic biodiversity along the floodplain. Other details of long-term samplings and sampling periods are provided in other publications (Soares et al., 2015; Dittrich, Dias, Bonecker, Lansac-Tôha & Padial, 2016; Ceschin, Bini & Padial, 2018). Therefore, to obtain more accurate and reliable trait values, intensive sampling was performed at 15 lakes (five in

each subsystem) in November 2015. Five "modules" were collected for each taxon in order to estimate traits mean value. A module was determined as the smaller repeated portion containing root, stem and leaves (Pérez-Harguindeguy et al., 2013). This approach was adopted in order to standardize samplings and due to the fact that most taxa have efficient vegetative propagation, making it difficult to separate individuals. All modules were packed in 100 L bags and maintained moistened until they were taken to the laboratory for traits measurements. For each module, 10 functional traits (Table 1) were measured, totaling 3.800 observations (5 modules x 76 taxa x 10 continuous traits). Other traits were obtained from information available in literature (Table 1). The mean of continuous traits plus the seven categorical traits obtained from the literature were used to generate a traits x taxon matrix (Supplementary Material 2).

Table 1. Functional traits chosen to describe aquatic macrophytes functional diversity, indicating if they were obtained from literature information or measured in the laboratory after sampling. See Supplemental Material 3 for details of chosen traits.

	CLASSIFICATION	TRAITS
OBTAINED FROM LITERATURE	Plant	*Amphibious*
		Emergent
		Epiphyte
		Fixed floating
		Free floating
		Fixed Submerged
		Free Submerged
		Annual
		Perennial
		Monthly blooming
		Semester blooming
		Annual blooming
	Leaf	*Glabrous pilosity*
		Pilous pilosity
		Coriaceous consistency
		Herbaceous consistency
	Stem	*Erect*

		Prostrate
	Root	*Fasciculate*
		Pivoting
MEASURED IN THE LABORATORY	Plant	*Height (cm)*
	Leaf	*Width (cm)*
		Length (cm)
		Thickness (mm)
	Petiole	*Length (mm)*
		Presence/ absence
	Stem	*Thickness (mm)*
		Presence/ absence
	Root	*Length (cm)*
		Presence/ absence

The abovementioned traits were chosen considering that they may reflect temporal variations based on the predictors used in this study (see Supplementary Material 3 for details). Indeed, traits related to morphology, growth and life form have been commonly used to describe how environmental conditions affect species reproduction, grow and survival (Cavalli, Baattrup-Pedersen & Riis, 2014). Related, morphologic traits have been successfully used as indicators of environmental conditions (Ali, Murphy & Abernethy, 1999). Unfortunately, we could not use physiologic traits given they are difficult to obtain (Zhang, 2004). Indeed, the inclusion of physiological traits would render research virtually unfeasible given the large effort involved and the expensive costs entailed (Petchey & Gaston, 2006), particularly considering the large number of species recorded in the UPRF. Still, we believe that the functional traits chosen are suitable proxies of how aquatic macrophytes vary over time. Also, we must highlight that by making a snapshot sampling for trait measurements, we could never capture temporal variation in intraspecific traits. In this case, intraspecific trait variation was only estimated by measuring different modules. Even so, given the strong trait differences among species, we do believe that our strategy is suitable to describe and explain (at least most of) aquatic macrophyte trait variation in the UPRF.

Data analyses

In order to assess floodplain FD, we followed recommendations of Mouillot, Graham, Villéger, Mason & Bellwood (2013) and estimated non-redundant FD indexes (we used FRic, FDiv, FDis and Rao's quadratic entropy). FRic (Functional Richness) measures functional richness considering all species in the community in order to build a multidimensional volume. Only extreme traits values are considered to estimate a convex hull. In FRic, variations in trait values within the convex are ignored. FDiv (Functional Divergence) is an index proposed to account for abundance and niche occupation of species. It is mathematically constructed to indicate high niche dissimilarity among species when FDiv values are high levels. FDis (Functional Dispersion) evaluates abundance-weighted distance of species mean trait values to the abundance-weighted mean trait values of the community. Last, RaoQ entropy (Rao's quadratic entropy) measures abundance-weighted sum of pairwise functional distances between species (see Box 2 in Mouillot, Graham, Villéger, Mason & Bellwood, 2013). Only RaoQ and FDis can be considered as the same "family", and may present redundant patterns (Mouillot, Graham, Villéger, Mason & Bellwood, 2013). Even so, we decided to keep both indexes given they are commonly used in studies.

The dbFD function of the R package of FD (Lalibertè & Legendre, 2010; Laliberté, Legendre & Shipley, 2014) was used to calculate the FD indexes. Matrices of taxon occurrences per sampling period and taxon traits were used and Gower distances were applied following Pavoine, Vallet, Dufour, Gachet & Daniel, (2009) in order to include and obtain a better mathematical approach for the 17 functional traits, and calculate multivariate distances between species based on the row trait data.

FD indexes (floodplain and subsystems) were generated for each sampling period for all of the UPRF sampling sites and subsystems (BA, IV and PR) sampling sites. Considering that functional dissimilarities are based on volume of convex hulls intersections in a multidimensional functional space, the "functional beta multi" function was applied to floodplain and the "functional beta pair" to the subsystem scale (as there were only two lakes within the subsystem) of the 'betapart' package (Baselga & Orme, 2012) in the R environment to access functional beta diversity. Two functional dissimilarities were measured that accounted for Simpson dissimilarity (turnover component of Sørensen dissimilarity-BetaSIM) and Sørensen dissimilarity (BetaSOR) (Baselga & Orme, 2012).

Species richness is commonly related to FD indexes (Heino, 2008; Bihn, Gebauer, & Brandl, 2010). Indeed, it was positively correlated with FRic for the floodplain and subsystem scale (r=0.59, P>0.001) and negatively correlated with FDis for the floodplain (r=-0.39, P=0.01) and Paraná subsystem (r=-0.40, P=0.01) (Supplementary Material 4). The increase in species number certainly contributes to the increase in new traits registered. An interesting relationship between species richness increase and FDiv decrease was found, providing an opportunity and platform for further research. Taking this into account, taxonomic species richness was not included as a predictor of FD. Our choice was based on the fact that the main interest is to explain temporal variation in diversity of likely "functions" performed by aquatic macrophytes in ecosystem, not controlling for the temporal variation in species taxonomic diversity (although we did consider this in the discussion section).

Temporal variation in FD indexes was explained by several predictors in the Generalized Least Squares model – GLS using the R package nmle (Pinheiro, Bates, Debroy & Sarkar, 2015). Inferences were based on the model-averaging approach,

considering models within a 95% confidence set (Greenland et al., 2016). We used GLS modeling approach given it had been shown suitable for data that have not only linear relationships, such as the ecological data used by us (see also Soares et al., 2015; Ceschin, Bini & Padial, 2018). Relatedly, predictor variables followed earlier publications that aimed to explain temporal variation in biodiversity of aquatic groups in the UPRF (Soares et al., 2015; Ceschin, Bini & Padial, 2018), and were made up of variables representing: environmental heterogeneity, nutrient availability, alkalinity, and hydrological regime, as described below.

The environmental heterogeneity (EH) of each sampling period was estimated using the analytical approach proposed by Anderson, Ellingsen, & Mcardle (2006) where a Principal Coordinates Analysis (PCoA) was applied to a standardized Euclidean matrix derived from the limnological variables, and the average distance of site locations to the centroid of a certain sampling period was used as a proxy of EH for the period. Alternatively, we also calculated the mean coefficient of variation of all limnological variables across sampling sites for each period (the CV variable). The limnological variables used were: water temperature (°C), dissolved oxygen ($mg \cdot L^{-1}$), pH, conductivity ($\mu S \cdot cm^{-1}$), Secchi disk depth (m), turbidity (NTU), inorganic suspended matter ($mg \cdot L^{-1}$), organic suspended matter ($mg \cdot L^{-1}$), chlorophyll-a ($\mu g \cdot L^{-1}$), total nitrogen ($\mu g \cdot L^{-1}$), and total phosphorus ($\mu g \cdot L^{-1}$) obtained from all sampling sites along the Long-Term Ecological Project. For more details see Roberto, Santana & Thomaz (2009).

Predictors related to the effect of nutrient availability on FD were based on previous studies dealing with the relationship between productivity and phosphorous and nitrogen concentration of different aquatic ecosystems (Vitousek, Mooney, Lubchenco & Melillo, 1997; Bozelli, Thomaz, Padial, Lopes & Bini, 2015). Therefore,

the mean value of total phosphorus ($\mu g \cdot L^{-1}$, Total-P) and nitrogen ($\mu g \cdot L^{-1}$, Total-N) were used across sampling sites as surrogates for nutrient availability during a sampling period. Alkalinity values (mg/L, ALK) were also obtained from the same Long Term Ecological Program and mean values were considered for floodplain and subsystem scale. This variable was not used in EH estimations given that it was correlated with the majority of the environmental variables with exception of dissolves oxygen and inorganic suspended material (Supplementary Material 5).

Two alternative approaches were used to generate hydrological regime predictors. Time-lagged hydrometric levels (HL10, HL20, HL30, HL40, HL50) were estimated in accordance with Soares et al. (2015) who proposed that the effect of the water level on communities may be ascribed to past water level variation (Thomaz, Bini & Bozelli, 2007; Soares et al., 2015). Therefore, the different time-lag numbers represent the days before samplings during which hydrometric levels were obtained (e.g., HL10 – water level 10 days before sampling). We also followed Ceshin, Bini & Padial (2018) and dug further into the representation of hydrological variation other than measurements of the water level. Flood events connect most lakes and tributaries in the UPRF when water levels exceed 3.5 m (Thomaz, Pagioro, Bini, Roberto & Rocha, 2004). As a consequence, the number of days since the last flood (NDF), duration of the last flood (DF) and DF/NDF ratio (closeness/intensity of the flood effect) were also used as hydrometric predictors.

For each GLS model, a combination of four explanatory variables (for floodplain or subsystem scales) was used: i) one representing environmental heterogeneity (EH or CV); ii) one representing nutrient availability (Total-N or Total-P); iii) one representing alkalinity; and iv) one representing the hydrological regime (HL10, HL20, HL30, HL40, HL50, NDF, DF or NDF/DF). In all models, we also included a vector ranging

from 1 to 38 called “TIME”, indicating a continuous temporal variation over the 38 periods, which represents a monotonic temporal trend. This variable was also used to control the temporal autocorrelation in the ‘nlme’ package (Pinheiro, Bates, Debroy & Sarkar, 2015) of the R environment. In our case, the best autocorrelation structure was the compound symmetry structure corresponding to a constant correlation (‘corCompSymm’; Pinheiro, Bates, Debroy & Sarkar, 2015). Given that more than one variable is an alternative representation of the predictors above, we calculated a total of 688 different GLS models; 172 considering the floodplain scale and 516 for subsystems (172 for each). Alternative models were compared using the Akaike Information Criterion (AIC) (Burnham & Anderson, 2002), and models with a delta AIC lower than 2 were considered equally suitable. Analyses were performed in the R environment (R Core Team, 2018), using ‘ade4’ (Dray, Dufour & Thioulouse, 2017), ‘vegan’ (Oksanen, Blanchet, Kindt, Legendre & Minchin, 2017), ‘MuMIn’ (Barton, 2017) and ‘nlme' (Pinheiro, Bates, Debroy & Sarkar, 2015) packages.

3. RESULTS

Functional diversity

FD indexes fluctuated considering all of the UPRF periods sampled (Fig. 1). However, FRic exhibited a visible temporal pattern (which is analyzed in GLS models, see below). Until June 2008, FRic was nearly constant with very few shifts. After then, a substantial increase followed by frequent non-monotonic oscillations can be clearly noticed.

Considering each subsystem separately, FRic also seems to increase over time for all of them, particularly after 2008. It should be noted that, in BA, FRic registered stability (2003-2008) with highly accentuated peaks and decays after 2008. On the other

hand, FDiv, FDis and RaoQ entropy seemed to decrease for the three subsystems, albeit with numerous peaks and decays (Fig. 2).

All indexes of functional beta diversity also oscillated with peaks and decays considering all sites in the UPRF and subsystems sites separately (Fig. 3).

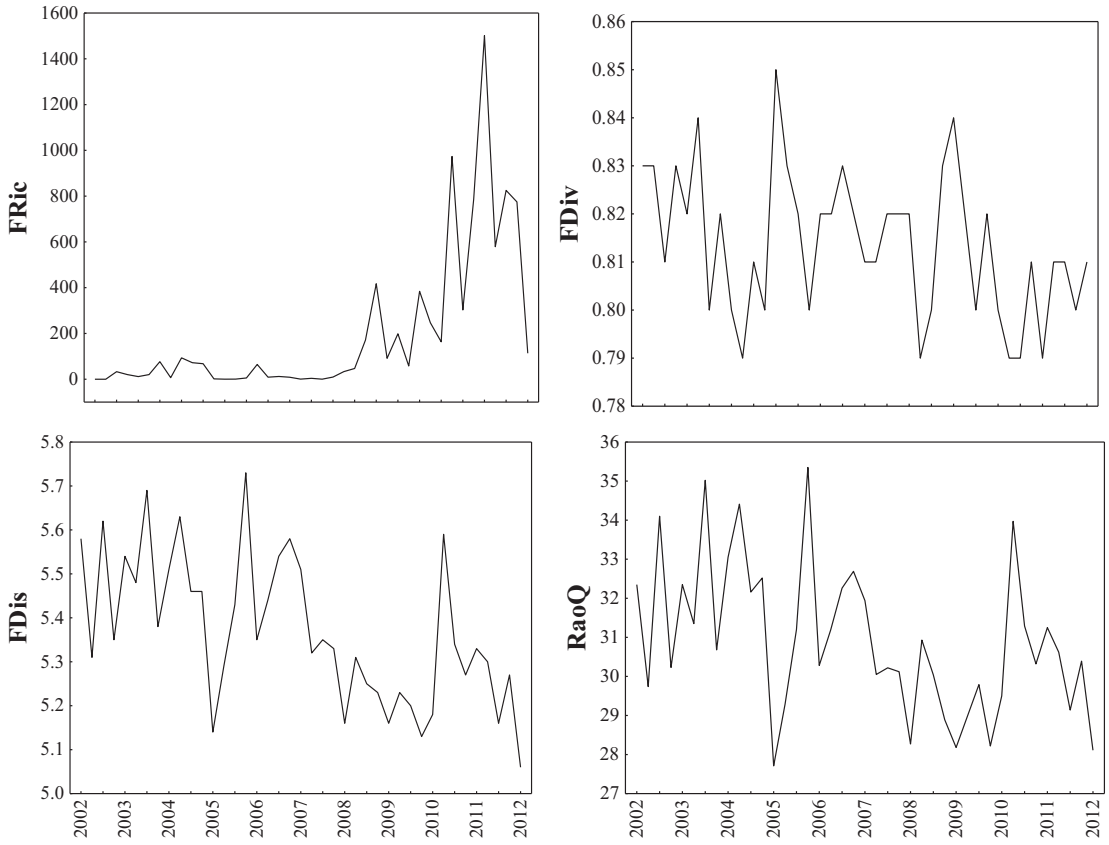

Figure 1 – Functional diversity indexes of the aquatic macrophytes communities during the 38 periods (11 years) for all UPRF sites sampled: FRic – functional richness; FDiv – functional divergence; FDis – functional dispersion; RaoQ – Rao's Quadratic entropy.

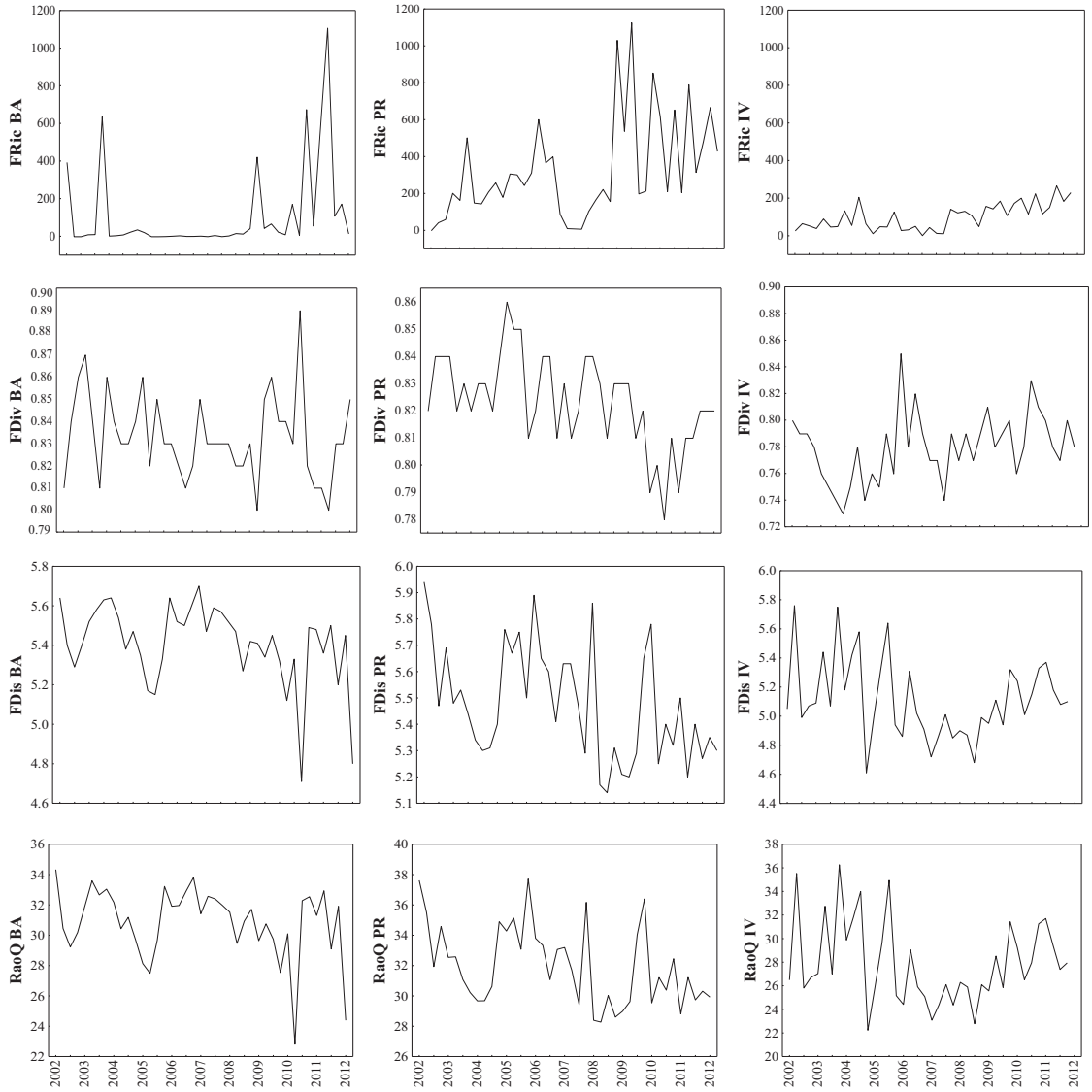

Figure 2 – Functional diversity indexes of the aquatic macrophytes communities during the 38 periods (11 years) for the PR, BA and IV subsystems. FRic – functional richness; FDiv – functional divergence; FDis – functional dispersion; RaoQ – Rao's quadratic entropy.

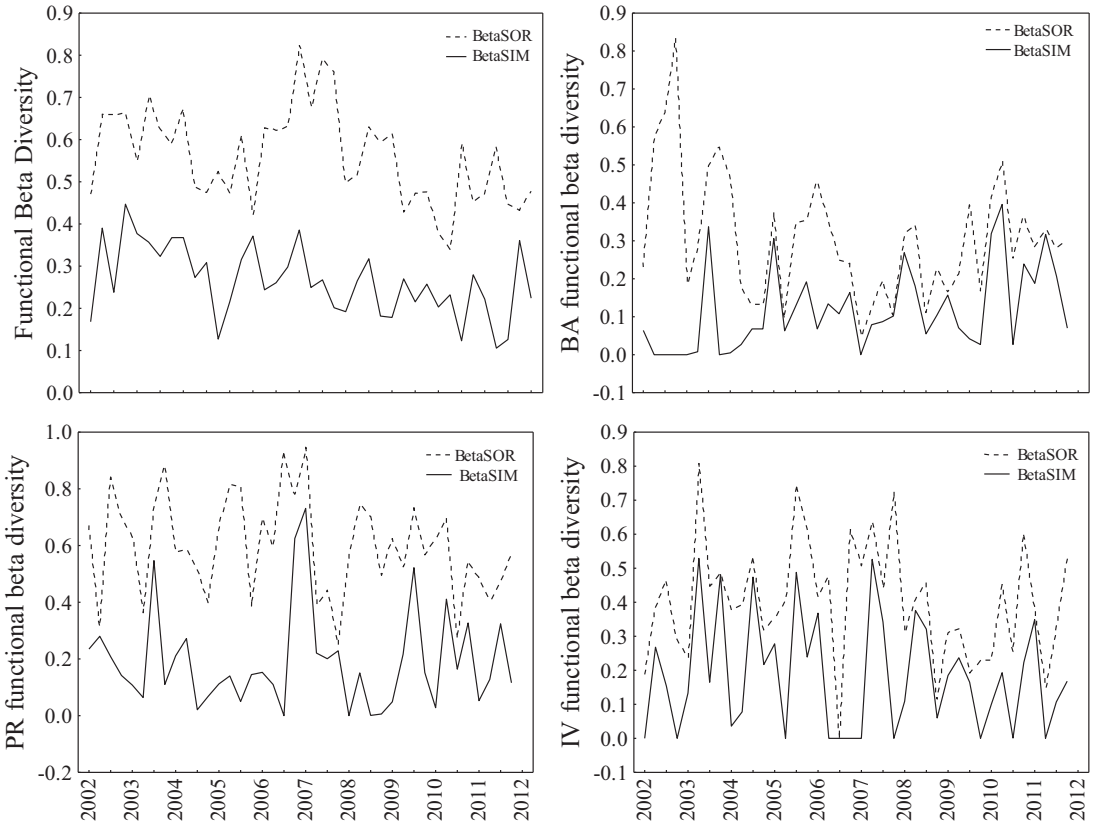

Figure 3 – Functional beta diversity (BetaSOR and BetaSIM) of the aquatic macrophytes communities in the Upper Paraná River floodplain (upper left graph), and in each subsystem (Baía – BA; Paraná – PR, Ivinheima – IV) during the 38 periods (11 years).

GLS Models

All model results are available in the Supplementary Material 6. In general terms, the number of suitable models for each index was high (reaching up to 20 models with delta AIC < 2, Table 2). However, significant variables in suitable models were usually the same (Table 2).

Table 2. Best GLS models summary results (with delta AIC < 2) of each predictor explaining functional diversity indexes (see acronyms in methods) of the aquatic macrophytes communities over the 38 periods (11 years). Coefficients and *P* values of significant predictors are shown only for the best model, and the number of models in which a predictor was significant / number of suitable models.

Scale	Indexes	N° models with ΔAIC<2	Significant predictors	Coefficient value of the best model	*P*
Floodplain	BetaSIM	20	TIME 24/24	-0.04	0.002
	BetaSOR	9	TIME 9/9	-0.03	0.01
			Total-P 9/9	0.07	<0.001
	FRic	4	TIME 4/4	1.96	<0.001
	FDiv	4	ALK 2/4	0.01	0.04
	FDis	6	TIME 6/6	-0.10	<0.001
			CV 2/6	-0.05	0.02
	RaoQ entropy	13	TIME 2/13	-0.88	0.005
Baia	BetaSIM	24	TIME 11/24	0.04	0.01
	BetaSOR	11	CV 5/11	-0.07	0.04
			TIME 10/11	-0.08	0.006
	FRic	3	TIME 1/3	78.00	0.05
	FDiv	-	-	-	-
	FDis	9	H10 1/9	0.09	0.04
			H20 1/9	0.09	0.04
			TIME 9/9	-0.10	0.005
	RaoQ entropy	9	H20 1/9	1.13	0.04
			TIME 2/9	-0.98	0.02
Paraná	BetaSIM	24	-	-	-
	BetaSOR	11	Total-P	0.06	0.04
	FRic	3	TIME 3/3	150.74	0.001
	FDiv	10	TIME 10/10	-0.01	<0.001
	FDis	12	Total-N 1/12	0.08	0.05
			TIME 12/12	-0.12	0.008
	RaoQ entropy	12	EH 4/12	-1.00	0.01
			Total-N 2/12	0.95	0.05
			TIME 12/12	-1.47	0.007
Ivinhema	BetaSIM	12	CV 12/12	0.06	0.02
	BetaSOR	12	Total-P 11/12	0.06	0.02
	FRic	2	TIME 2/2	-1.47	0.01
	FDiv	8	CV 8/8	-0.008	0.02
			H30 5/8	0.008	0.03
	FDis	6	Total-P 4/6	-0.10	0.03
			TIME 6/6	-0.12	0.01
	RaoQ entropy	2	TIME 2/2	-1.47	0.01

The variable "TIME" was positively related to only FRic; and negatively related to FDiv, FDis, RaoQ entropy, BetaSIM and BetaSOR considering all of the UPRF sites. Therefore, a temporal decrease regardless of other predictors was evidenced for these last indexes. The other significant relationship was between Total-P and BetaSOR (positive); ALK and FDiv (positive); and between CV and FDis (negative, see Table 2).

Considering each river separately, FRic and BetaSIM increased over time in BA; but FDis, Rao's quadratic entropy and BetaSOR decreased (Table 2). In this subsystem, time-lagged hydrometric levels HL10 and H20 were positively related to FDis, and H20 was positively related to RaoQ entropy. Finally, CV was negatively related to BetaSOR (Table 2).

In PR, FRic increased over time, while FDiv, FDis and RaoQ entropy decreased (Table 2). RaoQ entropy was also negatively related to EH (Table 2). Nutrient proxies were also positively related to some indexed: Total-P to BetaSOR; Total-N for FDis and RaoQ entropy (Table 2).

Contrarily for the other subsystems, FRic decreased over time in IV (Table 2). FDis and RaoQ entropy also decreased over time. FDis was also negatively related to total-P (Table 2); while was positively related to HL30 but negatively related to CV (Table 2). BetaSIM in IV was positively related to CV, and BetaSOR was positively related to Total-P (BetaSOR, Table 2).

4. DISCUSSION

Here, we showed temporal variation of different FD facets of aquatic macrophyte communities in a Neotropical floodplain during 11 years (38 periods). Long-term datasets allow one to assess reliable inferences considering FD (Lake, Bond & Reich, 2007), as well as its consequences on ecological communities and maintenance processes (Petchey & Gaston, 2006).

Even though our hypothesis that FD fluctuates according to several predictors has been partially confirmed, evidence of an overall increase or decrease depending on the functional index, contrary to our expectations, was obtained. A major result was the increase of the FRic index, while the other indexes decreased for the most part,

irrespective of the scale analyzed (using all of the UPRF sites, or only subsystem sites). The increase in FRic is in line with the identification bias postulated by Ferreira, Mormul, Thomaz, Pott & Pott (2011) who registered an increase in the number of aquatic macrophyte species identified in 2007 and 2009 resulting from a thorough taxonomic review of aquatic plants in the UPRF, in agreement with the period in which FRic increased the most (Figs. 1 and 2). FRic expresses the amount of niche space filled by species in the community, since it is measured as the convex hull volume that takes into account only the species with the most extreme trait values (Mouchet, Villéger, Mason & Mouillot, 2010; Mouillot, Graham, Villéger, Mason & Bellwood, 2013). If the new incoming trait values are extreme, they will certainly inflate the functional volume contributing directly to an increase in functional richness. The increase in FD has already been reported as a consequence of species richness increase (Petchey & Gaston, 2002). Although we could include species richness as a predictor to control for this bias in our modeling approach, the model selection could be affected, which could mask other relevant predictors of FD. Indeed, previous modeling exercise using species richness as a predictor resulted in the selection of models with this predictor only as relevant ($\Delta AIC < 2$).

Interestingly, such bias was accompanied by a scenario of homogenization of the other FD indexes. Surely, such result corroborates with Cadotte, Carscadden & Mirotchnick (2011) where species richness cannot be the only biodiversity measurement considered. New trait values in trait space could be located in either the center or the periphery of the trait space, and thus an increase in FRic may not be related to an increase in FDiv, for instance (Karadimou, Kallimanis, Tsiripidis & Dimopoulos, 2016). In line with this, different species could present traits mostly similar and then be considered functionally redundant even if one add little to the functional space

(Mouchet, Villéger, Mason & Mouillot, 2010). FDis and RaoQ entropy indicate how similar species are to each other inside the functional space of traits. Indeed species accumulation provides the dominance of certain traits which contribute to functional redundancy among species (Karadimou, Kallimanis, Tsiripidis & Dimopoulos, 2016). Therefore, one may expect that the taxonomic bias could cause a decrease in other FD indexes if non-recorded species were functionally similar. This is likely in the UPRF, given the large increase in the number of emergent and amphibian species after 2007 (Ferreira, Mormul, Thomaz, Pott & Pott 2011). Relatedly, the maintenance or even decrease in FDis and RaoQ entropy values reveals a likely increase in functional redundancy between the species (Karadimou, Kallimanis, Tsiripidis & Dimopoulos, 2016). On the other hand, a decrease in FD, if unrelated to a taxonomic bias, could also indicate a concerning scenario of biotic homogenization. In this case, the aquatic macrophytes assemblage homogenization could contribute to functional redundancy (Mormul, Esteves, Farjalla & Bozelli, 2015) and, thus, monitoring temporal trends in aquatic macrophyte communities are central.

Previous studies have demonstrated that redundant traits contribute similarly to ecosystem functionality (Fu et al., 2014) and to define functional groups (Naeem, 1998). Then, different species contributing similarly to ecosystem functionality (biochemical activities, atmospheric gases, nutrients, etc.) can be classified in the same functional group (Naeem, 1998). In this respect, redundant species increases ecosystem stability (Yachi & Loreau, 2009). Therefore, a higher accuracy in community lists cannot be a predictor of bias in ecosystem function proxies, given that simple “species addition” often occurs with high trait redundancy (Baiser & Lockwood, 2010). Our study reinforce that the taxonomic bias revealed high functional redundancy in the UPRF.

Even so, it is important to notice that the UPRF has been considerably affected by habitat alteration due to a dam construction that has decreased temporal variability in water level (Agostinho, Thomaz & Gomes, 2005), and by strong biological invasions events that have homogenized fish fauna (Vitule, Skóra & Abilhoa, 2012). Aquatic macrophyte occupation in the UPRF has also been affected considering the invasion of an aquatic macrophyte species very similar to a native counterpart (i.e., the invasive *Hydrilla verticillata* (L.f.) Royle and the native *Egeria najas* (Planch.) (Sousa, Thomaz, Murphy, Silveira & Mormul, 2009). These impacts certainly affect FD and deserve further attention and analyses. Changes in functional diversity is certainly a global concern (Clavel, Julliard & Devictor, 2011) that is likely to be caused by anthropogenic impacts such as those promoting biological invasions (Su, Xua, Akasaka, Molinos & Matsuzaki, 2015).

More than the monotonic temporal trends, we have also confirmed that FD can be partially explained by predictors tested here. As expected, the effects depend on the subsystem analyzed, as well as on the FD index evaluated. Evidence of the "flood homogenization hypothesis" (Thomaz, Bini & Bozelli, 2007) was generated for several groups in several floodplains (Johnson, Mudrak & Waller, 2014; Bozelli, Thomaz, Padial, Lopes & Bini, 2015; Opperman, Moyle, Larsen, Florsheim & Manfree, 2017). In this case, our study is the first to formally demonstrate relationships between hydrological regime proxies and FD indexes. Nonetheless, it is worth underlining that the relationships were contrary to our expectations due to the "flood homogenization hypothesis" – relationships between FD and hydrological regime proxies were usually positive. We can explain such result by the fact that the increase in water level may decrease ecological filtering of environmentally different sites, which can promote species colonization with traits not selected by local environmental conditions. Indeed,

with another set of data, Padial et al. (2014) have suggested that temporal variation related to water level may interact with environmental filtering of aquatic macrophyte community. Similarly, Lawson, Fryirs, Lenz & Leishman (2015) demonstrated that extreme flooding events associated with heterogeneous patterns of water flow promoted functional dispersion for macroinvertebrates. In addition, CV contributed negatively to FDis at a floodplain scale indicating that the variance in environmental variables promotes functional similarity at a broad scale.

As regards functional beta diversity at a floodplain scale, the predictor TIME was statistically significant though negatively for BetaSIM and BetaSOR along the 11 years, indicating a decrease of functional among-site dissimilarity. Total-P contributed positively to functional dissimilarity (BetaSOR) between rivers. In this sense, even though Total-P contributed to functional beta diversity (BetaSOR), its increase was not observed along the time. According to Roberto, Santana & Thomaz (2009), phosphorous concentrations are decreasing over time, which indicates an oligotrophication of the UPRF. As regards functional beta diversity, our results are in line with Chase & Leibold (2002) statement that, at a floodplain scale, beta diversity is positively related to productivity. Also, environmental variables were identified as the source of beta diversity variation of Cladoceran community structure at floodplain scale (Rocha, Heino, Machado-Velho, Lansac-Tôha & Lansac-Tôha, 2017). Even so, we cannot unlink these results with the taxonomic bias: it is expected that if non-recorded species were similar after efforts made by Ferreira, Mormul, Thomaz, Pott & Pott (2011); among-site variation in FD can also decrease.

It is also worth mentioning that the effects of the predictors, and so the likely mechanism to explain FD, depended on the subsystem. CV described negatively BetaSOR for Baia subsystem, though positively related to BetaSIM in Ivinhema.

Moreover, nutrient availability contributed to FD particularly in Paraná subsystem, possibly due to the natural productivity differences of such subsystems (Paraná is the least productive system; Roberto Santana & Thomaz, 2009). The differences in response described above evidence that changes in environmental variables among subsystems are central to explaining FD. In this regard, ecosystem functions are shown to be dependent on resource availability (Sutton-Grier, Wright, McGill & Richardson, 2011). Naturally, habitats are spatially diverse allowing species dissimilarity between sites due to niche differences that are represented in trait selection, which corroborates the hypothesis of environmental filtering (Simpson, 1949; Heino, Melo & Bini, 2015). Each species may develop within the best spectrum of a mosaic environment (Tilman, 2001). The relationship between ecosystem features and FD is thus central to understanding patterns in aquatic ecology (Palmer & Poff, 1997).

To sum up, the patterns in taxonomic biodiversity did not fully reflect the FD of aquatic macrophyte communities. Leaving FRic aside, which showed to be a species richness proxy, the lack of increase of the other indexes with respect to a biodiversity gain reveals functional homogenization through trait redundancy of previously unrecorded species. Such pattern is certainly important for conservation purposes, indicating that FD is a biodiversity facet that deserves to be evaluated in details, particularly in ecosystems subjected to intense anthropogenic impacts. The spatial scale associated with different environmental factors is also a key for FD drivers' comprehension. Finally, we may also conclude that, as well as for long-term patterns in taxonomic diversity (Soares et al., 2015; Ceschin, Bini & Padial, 2018), predictors of FD indexes are highly variable and context-dependent. Even so, it is clear that a better understanding of long-term ecosystem responses is reached only by investigating

taxonomic and functional facets of biodiversity together, using meaningful traits to avoid misinterpretations (Zhu et al. 2017).

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Supplementary Material 1 – List with taxonomic classification of the 76 aquatic macrophytes taxa sampled over 11 years at the Upper Paraná River Floodplain.

Family	**Genus**	**Species**
Acanthaceae	Hygrophylla	*Hygrophylla_costata*
Alismataceae	Echinodorus	*Echinodorus_sp*
Alismataceae	Limnocharis	*Limnocharis_sp*
Alismataceae	Sagittaria	*Sagittaria_sp*
Amaranthaceae	Alternanthera	*Alternanthera_sp*
Araceae	Lemna	*Lemna_valdiviana*
Araceae	Pistia	*Pistia_stratiotes*
Araceae	Wolffia	*Wolffia_sp*
Araceae	Wolfiella	*Wolffiella_lingulata*
Araceae	Wolfiella	*Wolffiella_oblonga*
Araliaceae	Hydrocotyle	*Hydrocotyle_ranunculoides*
Araliaceae	Hydrocotyle	*Hydrocotyle_sp*
Asteraceae	Eclipta	*Eclipta_prostrata*
Cabombaceae	Cabomba	*Cabomba_caroliniana*
Cabombaceae	Cabomba	*Cabomba_sp*
Ceratophyllaceae	Ceratophyllum	*Ceratophyllum_demersum*
Characeae	Chara	*Chara_sp*
Characeae	Nitella	*Nitella_furcata*
Commelinaceae	Commelina	*Commelina_sp*
Convolvulaceae	Ipomoea	*Ipomoea_sp*
Cyperaceae	Cyperus	*Cyperus_sp*
Cyperaceae	Eleocharis	*Eleocharis_sp*
Cyperaceae	Fuirena	*Fuirena_sp*
Cyperaceae	Oxycaryum	*Oxycaryum_cubense*
Cyperaceae	Rhynchospora	*Rhynchospora_sp*
Cyperaceae	Scleria	*Scleria_gaertneri*
Euphorbiaceae	Caperonia	*Caperonia_sp*
Fabaceae	Aeschynomene	*Aeschynomene_sensitiva*
Fabaceae	Mimosa	*Mimosa_setosa*
Haloragaceae	Myriophyllum	*Myriophyllum_aquaticum*
Pontederiaceae	Eichhornia	*Eichhornia_azurea*
Pontederiaceae	Eichhornia	*Eichhornia_crassipes*
Pontederiaceae	Pontederia	*Pontederia_cordata*
Pontederiaceae	Pontederia	*Pontederia_parviflora*
Pontederiaceae	Pontederia	*Pontederia_triflora*
Ricciaceae	Ricciocarpus	*Ricciocarpos_natans*
Rubiaceae	Diodia	*Diodia_sp*
Salviniaceae	Azolla	*Azolla_sp*
Salviniaceae	Salvinia	*Salvinia_sp*
Solanaceae	Solanum	*Solanum_glaucophyllum*
Solanaceae	Solanum	*Solanum_sp*
Thelypteridaceae	Thelypteris	*Cyclosorus_interruptus*
Typhaceae	Typha	*Typha_domingensis*
Xyridaceae	Xyris	*Xyris_sp*

Haloragaceae	Myriophyllum	*Myriophyllum_mattogrossensis*
Haloragaceae	Myriophyllum	*Myriophyllum_sp*
Hydrocharitaceae	Egeria	*Egeria_densa*
Hydrocharitaceae	Egeria	*Egeria_najas*
Hydrocharitaceae	Hydrilla	*Hydrilla_verticillata*
Hydrocharitaceae	Limnobium	*Limnobium_laevigatum*
Hydrocharitaceae	Najas	*Najas_microcarpa*
Hydroleaceae	Hydrolea	*Hydrolea_spinosa*
Lamiaceae	Hyptis	*Hyptis_sp*
Lentibulariaceae	Utricularia	*Utricularia_foliosa*
Lentibulariaceae	Utricularia	*Utricularia_gibba*
Linderniaceae	Lindernia	*Lindernia_rotundifolia*
Lythraceae	Cuphea	*Cuphea_sp*
Malvaceae	Hibiscus	*Hibiscus_sp*
Marantaceae	Thalia	*Thalia_geniculata*
Melastomataceae	Rynchantera	*Rhynchantera_sp*
Menyanthaceae	Nymphoides	*Nymphoides_indica*
Nymphaeaceae	Nymphaea	*Nymphaea_amazonum*
Onagraceae	Ludwigia	*Ludwigia_helminthorrhiza*
Onagraceae	Ludwigia	*Ludwigia_leptocarpa*
Onagraceae	Ludwigia	*Ludwigia_sp*
Orchidaceae	Habenaria	*Habenaria_sp*
Plantaginaceae	Bacopa	*Bacopa_salzmannii*
Poaceae	Urochloa	*Urochloa_mutica*
Poaceae	Hymenachne	*Hymenachne_amplexicaulis*
Poaceae	Leersia	*Leersia_hexandra*
Poaceae	Panicum	*Panicum_sp*
Poaceae	Paspalum	*Paspalum_repens*
Poaceae	Paspalum	*Paspalum_sp*
Poaceae	Urochloa	*Urochloa_arrecta*
Poaceae	Urochloa	*Urochloa_sp*
Polygonaceae	Polygonum	*Polygonum_sp*

Supplementary Material 2 – Database with taxa x traits considering categorical traits and mean values of continuous traits.

SPECIES	LIFEFORM	PERSISTENCE	BLOOMING	PILOSITY	LEAF CONSISTENCY	ROOT ARCHITECTURE	STEM ARCHITECTURE	HEIGHT (CM)	LEAF WIDTH (CM)	LEAF LENGTH (CM)	LEAF THICKNESS (MM)	STEM THICKNESS (MM)	PETIOLE LENGTH (MM)	ROOT LENGTH (CM)	PETIOLE P/A	STEM P/A	ROOT P/A
Aeschynomene_sensitiva	Amphibian	Perennial	Annual	Glabrous	Herbaceous	Pivoting	Erect	250.0	1.10	7.75	0.06	2.45	0.40	75.00	1	1	1
Alternanthera_sp	Amphibian	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Prostrate	300.0	3.25	8.50	0.12	5.54	0.60	17.00	1	1	1
Azolla_sp	Free_floating	Annual	NA	Glabrous	Herbaceous	Fasciculated	NA	0.20	2.25	2.00	2.00	0.00	0.00	1.25	0	0	1
Bacopa_salzmannii	Amphibian	Annual	Annual	Glabrous	Coriaceous	Pivoting	Erect	20.00	0.90	1.35	0.57	0.68	0.00	2.00	0	1	1
Brachiaria_mutica	Amphibian	Perennial	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	110.0	3.50	25.0	0.28	1.00	0.00	9.00	0	1	1
Cabomba_caroliniana	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Prostrate	157.50	3.95	2.40	0.12	1.14	1.10	5.75	1	1	1
Cabomba_sp	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Prostrate	300.0	3.80	2.40	0.11	1.64	1.50	18.00	1	1	1
Caperonia_sp	Amphibian	Perennial	Monthly	Pilous	Herbaceous	Fasciculated	Erect	100.0	1.15	8.75	0.17	3.23	0.25	67.32	1	1	1
Ceratophyllum_demersum	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Pivoting	Prostrate	210.0	1.85	2.50	0.23	0.20	0.00	19.50	0	1	1
Chara_sp	Fixed_submerged	Perennial	NA	Glabrous	Herbaceous	Pivoting	Prostrate	30.00	0.35	5.75	0.09	1.00	0.00	9.25	0	1	1
Commelina_sp	Amphibian	Annual	Semester	Glabrous	Herbaceous	Fasciculated	Prostrate	75.00	1.43	9.25	0.13	1.98	0.00	6.50	0	1	1
Cuphea_sp	Amphibian	Annual	Annual	Glabrous	Herbaceous	Pivoting	Erect	175.0	2.50	9.50	0.28	3.50	5.50	10.00	1	1	1
Cyperus_sp	Amphibian	Annual	Monthly	Glabrous	Coriaceous	Fasciculated	Erect	98.00	1.76	34.0	0.35	6.89	0.00	9.25	0	1	1
Diodia_sp	Amphibian	Annual	Annual	Glabrous	Coriaceous	Pivoting	Erect	35.00	2.25	1.10	0.45	33.00	3.25	7.50	1	1	1
Echinodorus_sp	Emergent	Annual	Semester	Glabrous	Coriaceous	Fasciculated	Erect	140.0	18.1	18.5	0.46	6.62	29.0	13.50	1	1	1

Eclipta_alba	Amphibian	Annual	Semester	Pilous	Coriaceous	Pivoting	Erect	45.00	1.80	8.40	0.17	2.44	0.00	7.15	0	1	1
Egeria_densa	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Erect	195.0	0.14	1.49	0.16	1.13	0.00	5.75	0	1	1
Egeria_najas	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Pivoting	Erect	250.0	0.15	1.50	0.18	1.11	0.00	5.00	0	1	1
Eichhornia_azurea	Fixed_floating	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Prostrate	58.00	24.0	12.5	0.60	16.50	180.0	57.50	1	1	1
Eichhornia_crassipes	Free_floating	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Prostrate	59.00	7.75	12.5	0.60	12.50	240.0	42.75	1	1	1
Eleocharis_sp	Emergent	Perennial	Annual	Glabrous	Herbaceous	Fasciculated	Erect	24.00	0.72	22.7	0.20	2.05	0.00	5.13	0	1	1
Fuirena_sp	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Prostrate	85.00	1.05	12.5	0.11	4.30	12.80	6.75	1	1	1
Habenaria_sp	Emergent	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Erect	35.00	1.85	17.5	0.18	2.90	0.00	15.00	0	1	1
Hibiscus_sp	Amphibian	Perennial	Semester	Pilous	Herbaceous	Fasciculated	Erect	180.00	8.80	15.6	0.28	3.55	21.75	11.75	1	1	1
Hydrilla_verticillata	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Erect	450.0	0.55	2.05	0.14	1.12	0.00	5.95	0	1	1
Hydrocotyle_sp	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	9.63	6.02	2.68	0.23	1.78	82.10	16.45	1	1	1
Hydrocotyle_ranunculoides	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	9.05	5.78	2.20	0.17	1.75	76.56	15.40	1	1	1
Hydrolea_spinosa	Amphibian	Perennial	Annual	Pilous	Herbaceous	Pivoting	Prostrate	75.00	1.55	9.75	0.17	8.50	20.00	16.00	1	1	1
Hygrophylla_costata	Amphibian	Annual	Annual	Pilous	Herbaceous	Pivoting	Erect	110.0	2.15	10.3	0.16	2.82	0.00	12.50	0	1	1
Hymenachne_amplexicaulis	Emergent	Perennial	Annual	Glabrous	Herbaceous	Fasciculated	Prostrate	175.00	3.60	30.0	0.17	10.25	0.00	17.50	0	1	1
Hyptis_sp	Amphibian	Annual	Semester	Pilous	Herbaceous	Pivoting	Erect	110.0	3.20	8.40	0.24	2.05	0.74	17.50	1	1	1
Ipomoea_sp	Epiphyte	Perennial	Annual	Pilous	Herbaceous	Pivoting	Erect	187.50	3.85	7.18	0.21	3.60	3.10	13.75	1	1	1
Leersia_hexandra	Amphibian	Perennial	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	110. 0	2.90	11.0	0.45	4.85	0.00	7.80	0	1	1
Lemna_valdiviana	Free_floating	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	NA	0.02	0.03	0.04	0.18	0.00	0.00	0.65	0	0	1
Limnobium_laevigatum	Free_floating	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Prostrate	6.50	3.85	3.85	4.65	2.65	44.00	33.00	1	1	1

Limnocharis_sp	Emergent	Annual	Semester	Glabrous	Coriaceous	Fasciculated	Erect	42.50	14.5	21.0	0.18	13.50	12.80	16.50	1	1	1
Lindernia_rotundifolia	Fixed_submerged	Annual	Annual	Glabrous	Coriaceous	Pivoting	Erect	25.00	2.30	3.10	0.17	1.88	0.80	8.25	1	1	1
Ludwigia_helminthorrhiza	Amphibian	Perennial	Annual	Glabrous	Coriaceous	Pivoting	Prostrate	3.10	3.60	3.55	0.30	4.75	12.50	10.25	1	1	1
Ludwigia_leptocarpa	Amphibian	Annual	Semester	Pilous	Herbaceous	Pivoting	Erect	150.0	3.43	13.5	0.12	4.50	4.00	23.00	1	1	1
Ludwigia_sp	Amphibian	Annual	Annual	Pilous	Herbaceous	Pivoting	Erect	146.25	1.32	8.06	0.12	3.13	4.71	16.88	1	1	1
Mimosa_setosa	Amphibian	Perennial	Semester	Glabrous	Herbaceous	Pivoting	Erect	160.0	0.45	1.45	0.16	5.00	5.50	85.00	1	1	1
Myriophyllum_brasiliensis	Fixed_submerged	Annual	Semester	Glabrous	Coriaceous	Pivoting	Erect	100.0	1.25	2.40	0.18	1.00	4.45	12.00	1	1	1
Myriophyllum_matogrossense	Fixed_submerged	Annual	Semester	Glabrous	Coriaceous	Pivoting	Erect	80.00	4.25	2.90	0.18	1.00	3.20	12.00	1	1	1
Myriophyllum_sp	Fixed_submerged	Annual	Semester	Glabrous	Coriaceous	Pivoting	Erect	50.00	0.45	2.55	0.24	0.87	4.00	16.00	1	1	1
Najas_microcarpa	Fixed_submerged	Annual	Monthly	Glabrous	Coriaceous	Pivoting	Erect	42.50	0.28	2.25	0.13	0.95	0.00	5.50	0	1	1
Nitella_furcata	Fixed_submerged	Annual	NA	Glabrous	Herbaceous	Pivoting	Erect	30.00	0.40	3.40	0.50	1.00	0.00	11.00	0	1	1
Nymphaea_amazonum	Fixed_floating	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Prostrate	250.0	22.5	22.5	0.58	45.00	250.0	19.50	1	1	1
Nymphoides_indica	Fixed_floating	Perennial	Semester	Glabrous	Coriaceous	Pivoting	Prostrate	37.50	7.90	7.75	0.29	34.00	15.00	87.50	1	1	1
Oxycaryum_cubense	Emergent	Annual	Monthly	Glabrous	Coriaceous	Fasciculated	Prostrate	55.00	2.37	67.5	0.22	1.95	0.00	7.75	0	1	1
Panicum_sp	Emergent	Annual	Monthly	Pilous	Herbaceous	Fasciculated	Erect	125.0	0.40	16.0	0.14	1.16	0.00	15.75	0	1	1
Paspalum_sp	Emergent	Annual	Semester	Pilous	Herbaceous	Fasciculated	Erect	20.00	3.75	13.7	0.10	0.50	0.00	16.80	0	1	1
Paspalum_repens	Emergent	Annual	Semester	Pilous	Herbaceous	Fasciculated	Erect	22.50	4.50	14.0	0.12	0.45	0.00	17.50	0	1	1
Pistia_stratiotes	Free_floating	Annual	Annual	Pilous	Coriaceous	Fasciculated	Prostrate	32.50	5.65	10.0	0.35	2.25	0.20	25.00	1	1	1
Polygonum_sp	Emergent	Perennial	Annual	Pilous	Herbaceous	Pivoting	Erect	107.92	2.73	14.1	0.23	13.64	18.59	17.64	1	1	1
Pontederia_cordata	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	110.0	7.25	19.0	0.20	42.50	59.00	20.50	1	1	1

Pontederia_parviflora	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	95.00	6.95	21.5	0.17	38.50	51.50	22.00	1	1	1
Pontederia_triflora	Emergent	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Erect	75.00	2.75	6.15	0.11	33.50	4.85	16.00	1	1	1
Rhynchospora_sp	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Pivoting	Erect	110. 0	0.68	49.2	0.32	4.11	0.00	8.13	0	1	1
Ricciocarpus_natans	Free_floating	Annual	NA	Glabrous	Herbaceous	Fasciculated	NA	0.30	0.55	1.25	2.75	0.00	0.00	0.55	0	0	1
Rynchantera_sp	Amphibian	Annual	Semester	Pilous	Herbaceous	Pivoting	Erect	195.0	3.40	6.25	0.16	14.50	12.80	18.50	1	1	1
Sagittaria_sp	Emergent	Annual	Semester	Glabrous	Herbaceous	Fasciculated	Erect	85.00	7.50	27.0	0.93	22.50	405.00	35.00	1	1	1
Salvinia_sp	Free_floating	Annual	NA	Pilous	Herbaceous	Fasciculated	Prostrate	1.03	1.68	1.47	0.72	0.08	0.15	3.55	1	1	1
Scleria_gaertneri	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Erect	70.00	3.29	15.0	0.26	1.35	0.00	6.75	0	1	1
Solanum_glaucophyllum	Amphibian	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Erect	150.0	1.60	2.25	0.27	0.19	1.05	18.50	1	1	1
Solanum_sp	Amphibian	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Erect	148.0	1.15	2.14	0.25	0.18	1.00	17.60	1	1	1
Thalia_geniculata	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Pivoting	Erect	325.0	6.50	45.0	0.21	150.0	925.0	21.50	1	1	1
Thelypteris_interrupta	Amphibian	Perennial	NA	Glabrous	Coriaceous	Fasciculated	Prostrate	85.00	1.55	13.0	0.09	3.17	12.80	6.50	1	1	1
Typha_domingensis	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Erect	300.0	1.75	125.	0.62	35.00	0.00	55.00	0	1	1
Urochloa_arrecta	Amphibian	Annual	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	110.0	1.75	11.5	0.18	0.35	0.00	17.50	0	1	1
Urochloa_sp	Amphibian	Annual	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	114.0	1.50	10.8	0.15	0.34	0.00	16.30	0	1	1
Utricularia_foliosa	Free_submerged	Annual	Annual	Glabrous	Herbaceous	Fasciculated	Prostrate	32.50	9.60	13.5	2.07	0.11	15.75	16.75	1	1	1
Utricularia_gibba	Free_submerged	Annual	Annual	Glabrous	Herbaceous	Fasciculated	Prostrate	16.00	4.75	5.66	0.10	0.03	0.00	1.75	0	1	1
Wolffia_sp	Free_floating	Annual	NA	Glabrous	Herbaceous	NA	NA	0.02	0.25	1.00	0.50	0.00	0.00	0.00	0	0	0
Wolfiella_lingulata	Free_floating	Annual	Semester	Glabrous	Herbaceous	NA	NA	0.02	0.17	0.28	0.20	0.00	0.00	0.00	0	0	0
Wolfiella_oblonga	Free_floating	Annual	Monthly	Glabrous	Herbaceous	NA	NA	0.02	0.05	0.38	0.20	0.00	0.00	0.00	0	0	0

Supplementary Material 3 – Chosen functional traits justification

Life form - species classification according to Pedralli (1990). The life form indicates the strategy of habitat adaptation were between aquatic macrophytes, species range from amphibious to totally submerse (Irgang & Gastal Jr. 1996).

Persistence - species classification in order to be annuals or perennial. The persistence time reveal the contribution of the organism to the ecosystem function (Pérez-Harguindeguy et al., 2013).

Blooming duration - the blooming duration reveal a greater reproductive success beyond the fact that the organism influences the rounding environment offering resources to the local biota in terms of seeds, fruit and biomass function (Pérez-Harguindeguy et al., 2013).

Height (cm) - measure made from the base line of the shoot to the upper photosynthetic region. This height measure reveals vigor and light competition between organisms (Westoby et al., 2002; Pérez-Harguindeguy et al., 2013).

Leaf width (cm) - measure of the wider portion of an imaginary circle on the leaf blade. According to Pérez-Harguindeguy et al., (2013) this measure have been considered as much efficient as leaf area in a way that with a greater surface contact area, the greater the canopy dominance.

Leaf length (cm) - measure of the longest portion of the leaf blade. This trait is supplementary to leaf width reflecting de surface contact area to canopy dominance (Pérez-Harguindeguy et al., 2013).

Leaf thickness (mm) - mean leaf thickness in 5 different points of the leaf blade excepting the main vein. This trait provides informations about the investment in cuticle, palisade and spongy parenchyma as well species strategies for resource acquisition and use (Kitajima & Poorter 2010).

Petiole length (mm) - measure of the total petiole length. This trait helps the leaf blade in the capture of light for the photosynthetic activity. We believe that longer petioles would contribute to a greater light absorption and consequently to a greater photosynthetic activity considering that petiole length and leaf blade length are highly associated (Abrahamson 2007).

Pilosity - the presence of trichomes at the leaf blade guarantee a micro climate around the stomata avoiding water loss (Brewer, Smith & Vogelmann 1991). Trichomes can also be efficient as mechanical barriers against herbivores, pathogens and intense light (Werker 2000) as well as reducer of radiation absorption reducing transpiration (Skelton et al., 2012).

Leaf consistency (cm) - the leaf texture reflects an efficient water economy strategy. This trait is supplementary to pilosity. We believe that leafs with a more coriaceous texture are more efficient in water economy due to the presence of a thick cuticle (Pérez-Harguindeguy et al., 2013).

Stem - diagnosis of stem being prostrated or erect resulting in more or less shade for neighboring organisms as well as wind exposure. According to Henry & Thomas (2002) taller plants growth on the occurrence of shade and/or no wind, while shorter plants growth on sun and/or wind exposure.

Stem thickness (mm) - measure of the middle part of the role stem length with the help of a digital pachymeter. The stem thickness reveals the efficiency on aerenchyma investment for better gas diffusion inside the plant (Pérez-Harguindeguy et al., 2013).

Root length (cm) - measure of the longest root. The root length indicates the need for nutrients. In this sense, we believe that a longer root will reveal a plant poorly supplied with nutrients while a shorter root will reveal a plant well supplied by nutrients around (Tabata et al., 2014)

Root architecture - diagnosis about the root being pivoting or fasciculate. Root architecture has already been associated to water availability (Fitter et al., 1991).

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Supplementary Material 4 - Correlation between taxonomic species richness and functional indexes for floodplain and subsystem scale. Bold results indicate statistic significance.

	Correlations	*P*	r
Floodplain	***S*-FRic**	**<0.001**	**0.59**
	S-FDiv	0.10	-0.26
	***S*-FDis**	**0.01**	**-0.39**
	S-Raoq	0.16	0.22
Subsytem Baia	***S*-FRic**	**0.01**	**0.39**
	S-FDiv	0.53	-0.10
	S-FDis	0.10	-0.27
	S-Raoq	0.30	-0.17
Subsytem Paraná	***S*-FRic**	**<0.001**	**0.59**
	***S*-FDiv**	**0.01**	**-0.40**
	***S*-FDis**	**0.009**	**-0.41**
	***S*-Raoq**	**0.02**	**-0.37**
Subsytem Ivinhema	***S*-FRic**	**<0.001**	**0.54**
	S-FDiv	0.05	-0.31
	S-FDis	0.26	-0.18
	S-Raoq	0.49	-0.11

Supplementary Material 5 – Correlation results among the variable Alkalinity and all environmental variables considered in the EH (environmanetl heterogeneity) and CV (coefficient variable) predictors. Bold results indicate statistic significance.

	Cor	*P*
Alkalinity + Deepness	**0.276**	**0.000**
Alkalinity + Air Temperature	**0.206**	**0.000**
Alkalinity + Water Temperature	**0.158**	**0.001**
Alkalinity + Dissolved oxygen 1	-0.026	0.593
Alkalinity + Dissolved oxygen 2	0.008	0.855
Alkalinity + pH	**0.440**	**0.000**
Alkalinity + CoNA	**0.795**	**0.000**
Alkalinity + Secchi	**0.410**	**0.000**
Alkalinity + Turb.	**-0.278**	**0.000**
Alkalinity + Total suspended material	**0.097**	**0.049**
Alkalinity + Inorganic suspended material	0.046	0.352
Alkalinity + Organic suspended material	**0.213**	**0.000**
Alkalinity + CLORO	**-0.199**	**0.000**
Alkalinity + N.A.	**-0.190**	**0.000**
Alkalinity + NO_3	**0.246**	**0.000**
Alkalinity + NH_4	**-0.152**	**0.001**
Alkalinity + Total phosphorous	**-0.348**	**0.000**
Alkalinity + PO_4	**-0.101**	**0.039**

Supplementary Material 6 - General Linear Models of the Floodplain and Subsystems scale. Bold results indicate statistic significance. CV = coefficient of significance; EH = environmental heterogeneity; Total-P = mean phosphorous concentration; Total-N = mean nitrogen concentration; ALK = alkalinity; HL10/20/30/40 or 50 = water level x days before sampling; NDF = number of days since the last flood; DF = duration of the last flood; DF/NDF ratio (closeness/intensity of the flood effect); TIME = 38 sampling periods.

General Linear Models of the UPRF

Functional BetaSIM GLS models with ΔAIC<2.

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: -44.69 ΔAIC: 0 wi: 0.05	CV	-0.01	-1.02	0.31
		Total-N	-0.01	-0.61	0.54
		H10	0.006	0.50	0.61
		TIME	**-0.03**	**-2.27**	**0.02**
2	AIC: -44.55 ΔAIC: 0.14 wi: 0.05	CV	-0.01	-0.93	0.35
		Total-N	-0.01	-0.76	0.45
		ALK	0.003	0.27	0.78
		TIME	**-0.03**	**-2.14**	**0.003**
3	AIC: -44.48 ΔAIC: 0.20 wi: 0.05	CV	-0.01	-0.97	0.33
		Total-N	-0.01	-0.65	0.51
		H20	0.003	0.28	0.77
		TIME	**-0.03**	**-2.21**	**0.03**
4	AIC: -44.48 ΔAIC: 0.21 wi: 0.05	EH	-0.01	-0.90	0.37
		Total-N	-0.01	-0.72	0.47
		H50	-0.005	0.39	0.69
		TIME	**-0.03**	**-2.02**	**0.05**
5	AIC: -44.41 ΔAIC: 0.28 wi: 0.05	CV	-0.01	-0.94	0.35
		Total-N	-0.01	-0.68	0.49
		H30	0.001	0.11	0.91
		TIME	**-0.03**	**-2.15**	**0.03**
6	AIC: -44.39 ΔAIC: 0.30 wi: 0.04	CV	-0.01	-0.93	0.35
		Total-N	-0.01	-0.71	0.47
		H50	-0.001	-0.09	0.92
		TIME	**-0.03**	**-2.11**	**0.04**
7	AIC: -44.38 ΔAIC: 0.31 wi: 0.04	CV	-0.01	-0.93	0.35
		Total-N	-0.01	-0.69	0.49
		H40	<0.001	0.04	0.96
		TIME	**-0.03**	**-2.15**	**0.03**
8	AIC: -44.37 ΔAIC: 0.32 wi: 0.04	EH	-0.01	-0.78	0.43
		Total-N	-0.01	-0.72	0.47
		ALK	0.002	0.15	0.87
		TIME	**-0.03**	**-2.10**	**0.04**
9	AIC: -44.36	EH	-0.01	-0.86	0.40

	ΔAIC: 0.33 wi: 0.04	Total-N	-0.01	-0.72	0.47
		H40	-0.003	-0.25	0.80
		TIME	**-0.03**	**-2.06**	**0.05**
10	AIC: -44.30 ΔAIC: 0.38 wi: 0.05	EH	-0.01	-0.83	0.40
		Total-N	-0.01	-0.72	0.47
		H30	-0.002	-0.18	0.85
		TIME	**-0.03**	**-2.06**	**0.04**
11	AIC: -44.29 ΔAIC: 0.40 wi: 0.04	EH	-0.01	-0.79	0.43
		Total-N	-0.01	-0.71	0.48
		H10	0.002	0.21	0.83
		TIME	**-0.03**	**-2.15**	**0.03**
12	AIC: -44.23 ΔAIC: 0.46 wi: 0.04	EH	-0.01	-0.80	0.42
		Total-N	-0.01	-0.72	0.47
		H20	<0.001	0.007	0.99
		TIME	**-0.03**	**-2.11**	**0.04**
13	AIC: -44.01 ΔAIC: 0.68 wi: 0.04	CV	-0.01	-1.29	0.20
		Total-P	<0.001	0.06	0.94
		H10	0.008	0.62	0.53
		TIME	**-0.04**	**-3.23**	**0.002**
14	AIC: -43.74 ΔAIC: 0.95 wi: 0.03	CV	-0.02	-1.22	0.22
		Total-P	< -0.001	<-0.001	1.00
		H20	0.005	0.37	0.70
		TIME	**-0.04**	**-3.17**	**0.003**
15	AIC: -43.63 ΔAIC: 1.06 wi: 0.03	CV	-0.01	-1.18	0.24
		Total-P	< -0.001	-0.04	0.96
		H30	0.002	0.20	0.84
		TIME	**-0.04**	**-3.13**	**0.003**
16	AIC: -43.62 ΔAIC: 1.07 wi: 0.03	EH	-0.01	-1.14	0.25
		Total-P	-0.001	-0.20	0.84
		H50	<0.001	-0.41	0.68
		TIME	**-0.03**	**-2.87**	**0.006**
17	AIC: -43.58 ΔAIC: 1.10 wi: 0.03	CV	-0.01	-1.16	0.25
		Total-P	-0.001	-0.08	0.93
		H50	0.001	0.001	0.99
		TIME	**-0.03**	**-3.11**	**0.003**
18	AIC: -43.58 ΔAIC: 1.10 wi: 0.03	CV	-0.01	-1.17	0.24
		Total-P	<-0.001	-0.05	0.95
		H40	0.001	0.13	0.89
		TIME	**-0.04**	**-3.13**	**0.003**
19	AIC: -43.57 ΔAIC: 1.12 wi: 0.03	CV	-0.01	-1.16	0.25
		Total-P	-0.001	-0.09	0.92
		ALK	<0.001	0.02	0.97
		TIME	**-0.03**	**-3.12**	**0.003**
20	AIC: -43.49 ΔAIC: 1.20 wi: 0.03	EH	-0.01	-1.11	0.27
		Total-P	-0.002	-0.17	0.86
		H40	-0.003	-0.26	0.79
		TIME	**-0.03**	**-2.90**	**0.006**

21	AIC: -43.43 ΔAIC: 1.26 wi: 0.03	EH	-0.01	-1.09	0.28
		Total-P	-0.002	-0.17	0.86
		H30	-0.002	-0.18	0.85
		TIME	**-0.03**	**-2.90**	**0.006**
22	AIC: -43.42 ΔAIC: 1.27 wi: 0.03	EH	-0.01	-1.09	0.28
		Total-P	-0.002	-0.17	0.86
		H10	-0.002	-0.18	0.85
		TIME	**-0.03**	**-2.90**	**0.006**
23	AIC: -43.39 ΔAIC: 1.30 wi: 0.03	EH	-0.01	-1.07	0.28
		Total-P	-0.001	-0.11	0.91
		ALK	-0.001	-0.10	0.92
		TIME	**-0.03**	**-2.99**	**0.005**
24	AIC: -43.36 ΔAIC: 1.33 wi: 0.02	EH	-0.01	-1.07	0.28
		Total-P	0.002	-0.15	0.88
		ALK	<0.001	0.01	0.99
		TIME	**-0.03**	**-2.97**	**0.005**

Functional BetaSOR GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: -33.19 ΔAIC: 0 wi: 0.14	CV	-0.02	-0.98	0.33
		Total-P	**0.06**	**4.19**	**<0.001**
		H20	0.02	1.71	0.09
		TIME	**-0.03**	**-2.60**	**0.01**
2	AIC: -33.14 ΔAIC: 0.04 wi: 0.14	CV	-0.01	-1.03	0.30
		Total-P	**0.07**	**4.19**	**<0.001**
		H10	0.02	1.68	0.10
		TIME	**-0.03**	**-2.63**	**0.01**
3	AIC: -32.88 ΔAIC: 0.30 wi: 0.12	EH	-0.01	-0.85	0.40
		Total-P	**0.06**	**4.18**	**<0.001**
		H20	0.02	1.44	0.15
		TIME	**-0.03**	**-2.45**	**0.01**
4	AIC: -32.78 ΔAIC: 0.40 wi: 0.12	EH	-0.01	-0.89	0.37
		Total-P	**0.06**	**4.18**	**<0.001**
		H10	0.02	1.39	0.17
		TIME	**-0.03**	**-2.45**	**0.01**
5	AIC: -32.15 ΔAIC: 1.03 wi: 0.09	CV	-0.01	-0.83	0.40
		Total-P	**0.06**	**4.05**	**<0.001**
		H30	0.02	1.35	0.18
		TIME	**-0.03**	**-2.53**	**0.01**
6	AIC: -32.04 ΔAIC: 1.14 wi: 0.08	EH	-0.01	-0.77	0.44
		Total-P	**0.06**	**4.09**	**<0.001**
		H30	0.01	1.07	0.29
		TIME	**-0.03**	**-2.35**	**0.02**
7	AIC: -31.50 ΔAIC: 1.69	EH	-0.01	-0.75	0.45
		Total-P	**0.06**	**4.02**	**<0.001**

	wi: 0.06	H40	0.01	0.74	0.45
		TIME	**-0.03**	**-2.25**	**0.03**
8	AIC: -31.40 ΔAIC: 1.79 wi: 0.06	CV	-0.01	-0.71	0.48
		Total-P	**0.06**	**3.93**	**<0.001**
		H40	0.01	1.03	0.30
		TIME	**-0.03**	**-2.42**	**0.02**
9	AIC: -31.27 ΔAIC: 1.91 wi: 0.05	EH	-0.01	-0.77	0.44
		Total-P	**0.06**	**3.99**	**<0.001**
		H40	0.009	0.56	0.58
		TIME	**-0.03**	**-2.20**	**0.03**

Functional Richness (FRic) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 495.36 ΔAIC: 0 wi: 0.32	EH	10.56	0.19	0.84
		Total-N	-56.57	-0.87	0.38
		NDF	-48.75	-0.98	0.33
		DF	-31.17	-0.31	0.75
		NDF/DF	-16.99	-0.18	0.85
		TIME	**229.51**	**3.81**	**<0.001**
2	AIC: 495.55 ΔAIC: 0.18 wi: 0.29	CV	5.39	0.10	0.91
		Total-N	-53.36	-0.84	0.40
		NDF	-49.15	-0.98	0.33
		DF	-35.93	-0.37	0.70
		NDF/DF	-15.93	-0.16	0.86
		TIME	**228.44**	**3.77**	**<0.001**
3	AIC: 496.48 ΔAIC: 1.12 wi: 0.18	CV	-22.69	-0.43	0.66
		Total-P	16.70	0.30	0.76
		NDF	-69.39	-1.39	0.17
		DF	-53.86	-0.56	0.57
		NDF/DF	-0.31	-0.003	0.99
		TIME	**196.48**	**4.23**	**<0.001**
4	AIC: 496.51 ΔAIC: 1.15 wi: 0.18	EH	-19.63	-0.37	0.71
		Total-P	13.16	0.25	0.80
		NDF	-67.41	-1.36	0.18
		DF	-55.23	-0.56	0.57
		NDF/DF	-5.46	-0.05	0.95
		TIME	**197.43**	**4.20**	**<0.001**

Functional Divergence (FDiv) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*

1	AIC: -159.48 ΔAIC: 0 wi: 0.16	EH	-0.003	-0.52	0.60
		Total-N	0.002	0.27	0.78
		ALK	0.009	1.41	0.16
		TIME	0.001	0.23	0.81
2	AIC: -159.47 ΔAIC: 0.008 wi: 0.16	CV	-0.002	-0.36	0.71
		Total-P	-0.008	-1.23	0.22
		ALK	**0.01**	**2.08**	**0.04**
		TIME	0.001	0.19	0.84
3	AIC: -159.18 ΔAIC: 0.30 wi: 0.14	CV	-0.007	-1.05	0.29
		Total-N	0.003	0.44	0.65
		ALK	0.01	1.51	0.13
		TIME	0.001	0.13	0.88
4	AIC: -159.12 ΔAIC: 0.35 wi: 0.14	EH	0.001	0.22	0.82
		Total-P	-0.01	-1.47	0.15
		ALK	**0.01**	**2.09**	**0.04**
		TIME	<0.001	0.06	0.94

Functional Dispersion (FDis) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: -6.38 ΔAIC: 0 wi: 0.14	CV	-0.04	-1.68	0.10
		Total-N	-0.02	-0.80	0.42
		H10	0.03	1.63	0.11
		TIME	**-0.08**	**-3.23**	**0.002**
2	AIC: -5.83 ΔAIC: 0.55 wi: 0.10	**CV**	**-0.05**	**-2.29**	**0.02**
		Total-P	0.01	0.63	0.52
		H10	0.04	1.89	0.06
		TIME	**-0.10**	**-4.47**	**<0.001**
3	AIC: -5.34 ΔAIC: 1.04 wi: 0.08	CV	-0.03	-1.55	0.12
		Total-N	-0.02	-0.88	0.38
		H20	0.02	1.26	0.21
		TIME	**-0.08**	**-3.07**	**0.004**
4	AIC: -4.62 ΔAIC: 1.75 wi: 0.06	CV	-0.03	-1.44	0.15
		Total-N	-0.02	-0.92	0.35
		H30	0.02	0.92	0.35
		TIME	**-0.08**	**-2.95**	**0.005**
5	AIC: -4.51 ΔAIC: 1.86 wi: 0.05	**CV**	**-0.05**	**-2.12**	**0.04**
		Total-P	0.01	0.50	0.61
		H20	0.03	1.48	0.14
		TIME	**-0.09**	**-4.29**	**<0.001**
6	AIC: -4.40 ΔAIC: 1.97 wi: 0.05	EH	-0.02	-0.87	0.38
		Total-N	-0.03	-1.12	0.26
		H10	0.02	1.16	0.25
		TIME	**-0.08**	**-2.92**	**0.006**

Rao's quadratic Entropy GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 168.04 ΔAIC: 0 wi: 0.10	CV	-0.41	-1.33	0.19
		Total-N	-0.47	-1.24	0.22
		H10	-0.33	1.14	0.26
		TIME	**-0.63**	**-1.75**	**0.008**
2	AIC: 168.74 ΔAIC: 0.69 wi: 0.07	CV	-0.34	-1.11	0.27
		Total-N	-0.44	-1.09	0.28
		ALK	-0.22	-0.74	0.46
		TIME	-0.54	-1.56	0.12
3	AIC: 168.74 ΔAIC: 0.70 wi: 0.07	CV	-0.38	-1.22	0.22
		Total-N	-0.49	-1.31	0.19
		H20	0.23	0.78	0.43
		TIME	-0.58	-1.62	0.11
4	AIC: 169.06 ΔAIC: 1.10 wi: 0.06	EH	-0.26	-0.83	0.41
		Total-N	-0.45	-1.07	0.28
		ALK	-0.26	-0.84	0.40
		TIME	-0.52	-1.49	0.14
5	AIC: 169.20 ΔAIC: 1.15 wi: 0.05	EH	-0.26	-0.83	0.41
		Total-N	-0.45	-1.07	0.28
		ALK	-0.26	-0.84	0.40
		TIME	-0.52	-1.49	0.14
6	AIC: 169.27 ΔAIC: 1.22 wi: 0.05	CV	-0.34	-1.11	0.27
		Total-N	-0.52	-1.37	0.17
		H40	0.09	0.32	0.74
		TIME	-0.53	-1.49	0.14
7	AIC: 169.32 ΔAIC: 1.28 wi: 0.05	CV	-0.34	-1.10	0.27
		Total-N	-0.53	-1.38	0.17
		H50	0.06	0.22	0.82
		TIME	-0.52	-1.46	0.15
8	AIC: 169.38 ΔAIC: 1.34 wi: 0.05	EH	-0.19	-0.62	0.53
		Total-N	-0.58	-1.52	0.13
		H10	0.23	0.79	0.43
		TIME	-0.54	-1.52	0.13
9	AIC: 169.78 ΔAIC: 1.74 wi: 0.04	EH	-0.20	-0.63	0.53
		Total-N	-0.59	-1.53	0.13
		H20	0.14	0.48	0.63
		TIME	-0.51	-1.43	0.16
10	AIC: 169.79 ΔAIC: 1.74 wi: 0.04	CV	-0.63	-1.93	0.06
		Total-P	0.09	0.29	0.77
		H10	0.42	1.38	0.17
		TIME	**-0.88**	**-2.97**	**0.005**
11	AIC: 169.90 ΔAIC: 1.86 wi: 0.04	EH	-0.20	-0.62	0.53
		Total-N	-0.59	-1.54	0.13
		H30	0.07	0.26	0.79

		TIME	-0.49	-1.38	0.17
12	AIC: 169.92 ΔAIC: 1.88 wi: 0.04	EH	-0.22	-0.67	0.50
		Total-N	-0.59	-1.54	0.13
		H50	-0.01	-0.03	0.97
		TIME	-0.47	-1.31	0.19
13	AIC: 169.94 ΔAIC: 1.89 wi: 0.04	EH	-0.21	-0.65	0.51
		Total-N	-0.59	-1.54	0.13
		H40	0.02	0.06	0.94
		TIME	-0.48	-1.33	0.18

General Linear Models of the BAIA SUBSYSTEM

Functional BetaSIM GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: -19.76 ΔAIC: 0 wi: 0.06	CV	-0.02	-1.06	0.29
		Total-P	0.02	1.11	0.27
		H10	0.02	1.13	0.26
		TIME	0.03	1.92	0.06
2	AIC: -19.56 ΔAIC: 0.19 wi: 0.06	EH	0.008	0.40	0.68
		Total-P	0.01	0.58	0.56
		ALK	0.02	1.21	0.26
		TIME	**0.04**	**2.21**	**0.03**
3	AIC: -19.53 ΔAIC: 0.22 wi: 0.06	CV	-0.01	-0.55	0.58
		Total-P	0.01	0.59	0.55
		ALK	0.02	1.30	0.20
		TIME	**0.04**	**2.46**	**0.01**
4	AIC: -19.49 ΔAIC: 0.26 wi: 0.06	CV	-0.009	-0.51	0.61
		Total-N	0.007	0.33	0.73
		ALK	0.02	1.40	0.16
		TIME	0.03	1.83	0.07
5	AIC: -19.47 ΔAIC: 0.29 wi: 0.05	EH	0.006	0.30	0.75
		Total-N	0.006	0.30	0.76
		ALK	0.02	1.33	0.19
		TIME	0.03	1.66	0.10
6	AIC: -19.43 ΔAIC: 0.32 wi: 0.05	CV	-0.02	-0.98	0.33
		Total-N	0.01	0.80	0.42
		H10	0.02	1.09	0.28
		TIME	0.02	0.99	0.32
7	AIC: -19.38 ΔAIC: 0.37 wi: 0.05	CV	-0.02	-0.90	0.36
		Total-P	0.02	1.11	0.27
		H20	0.02	0.88	0.38
		TIME	**0.04**	**2.05**	**0.04**
8	AIC: -19.01 ΔAIC: 0.74	CV	-0.01	-0.73	0.46
		Total-P	0.02	1.05	0.29

	wi: 0.04	H30	0.01	0.66	0.51
		TIME	**0.04**	**2.12**	**0.04**
9	AIC: -18.93 ΔAIC: 0.82 wi: 0.04	CV	-0.02	-0.77	0.44
		Total-N	0.01	0.75	0.45
		H20	0.02	0.77	0.44
		TIME	0.02	1.13	0.26
10	AIC: -18.62 ΔAIC: 1.14 wi: 0.03	CV	-0.01	-0.49	0.62
		Total-P	0.01	0.95	0.34
		H40	0.008	0.31	0.75
		TIME	**0.04**	**2.34**	**0.02**
11	AIC: -18.57 ΔAIC: 1.19 wi: 0.03	CV	-0.01	-0.58	0.56
		Total-N	0.01	0.67	0.50
		H30	0.01	0.52	0.60
		TIME	0.03	1.25	0.21
12	AIC: -18.51 ΔAIC: 1.25 wi: 0.03	CV	-0.01	-0.40	0.69
		Total-P	0.01	0.90	0.36
		H50	0.004	0.18	0.85
		TIME	**0.04**	**2.39**	**0.02**
13	AIC: -18.40 ΔAIC: 1.35 wi: 0.03	EH	0.06	0.29	0.77
		Total-P	0.01	0.88	0.38
		H10	0.008	0.41	0.68
		TIME	**0.04**	**2.21**	**0.03**
14	AIC: -18.26 ΔAIC: 1.49 wi: 0.03	EH	0.008	0.36	0.71
		Total-P	0.01	0.91	0.36
		H20	0.003	0.16	0.86
		TIME	**0.04**	**2.26**	**0.03**
15	AIC: -18.26 ΔAIC: 1.49 wi: 0.03	EH	0.01	0.51	0.60
		Total-P	0.01	0.91	0.36
		H50	-0.005	-0.26	0.79
		TIME	**0.04**	**2.28**	**0.02**
16	AIC: -18.24 ΔAIC: 1.51 wi: 0.03	CV	-0.008	-0.32	0.74
		Total-N	0.01	0.58	0.56
		H40	0.004	0.16	0.87
		TIME	0.03	1.46	0.15
17	AIC: -18.22 ΔAIC: 1.53 wi: 0.03	EH	0.01	0.49	0.62
		Total-P	0.01	0.92	0.36
		H40	-0.003	-0.18	0.85
		TIME	**0.04**	**2.28**	**0.02**
18	AIC: -18.22 ΔAIC: 1.54 wi: 0.03	EH	0.009	0.42	0.67
		Total-P	0.01	0.92	0.36
		H30	0.0007	0.003	0.97
		TIME	**0.04**	**2.26**	**0.03**
19	AIC: -18.15 ΔAIC: 1.61 wi: 0.03	CV	-0.005	-0.22	0.82
		Total-N	0.01	0.54	0.58
		H50	-0.001	0.009	0.99
		TIME	0.03	1.55	0.12

20	AIC: -18.11 ΔAIC: 1.65 wi: 0.03	EH	0.003	0.15	0.88
		Total-N	0.01	0.55	0.58
		H10	0.009	0.48	0.62
		TIME	0.03	1.48	0.14
21	AIC: -17.93 ΔAIC: 1.82 wi: 0.02	EH	0.008	0.39	0.69
		Total-N	0.01	0.55	0.58
		H50	-0.005	-0.30	0.76
		TIME	0.03	1.54	0.13
22	AIC: -17.92 ΔAIC: 1.83 wi: 0.02	EH	0.004	0.22	0.82
		Total-N	0.01	0.55	0.58
		H20	0.004	0.20	0.83
		TIME	0.03	1.51	0.13
23	AIC: -17.88 ΔAIC: 1.88 wi: 0.02	EH	0.007	0.33	0.71
		Total-N	0.01	0.55	0.58
		H40	-0.003	-0.19	0.84
		TIME	0.03	1.53	0.13
24	AIC: -17.87 ΔAIC: 1.88 wi: 0.02	EH	0.006	0.28	0.77
		Total-N	0.01	0.55	0.57
		H30	<0.001	0.04	0.96
		TIME	0.03	1.52	0.13

Functional BetaSOR GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 4.44 ΔAIC: 0 wi: 0.09	CV	-0.07	-1.93	0.06
		Total-N	-0.009	-0.31	0.75
		H10	0.04	1.15	0.25
		TIME	**-0.07**	**-2.28**	**0.02**
2	AIC: 4.61 ΔAIC: 0.17 wi: 0.08	CV	-0.06	-1.84	0.07
		Total-N	-0.009	-0.30	0.76
		H30	0.03	1.05	0.29
		TIME	**-0.07**	**-2.22**	**0.03**
3	AIC: 4.71 ΔAIC: 0.28 wi: 0.08	**CV**	**-0.07**	**-2.10**	**0.04**
		Total-N	0.006	0.24	0.81
		H30	0.04	1.28	0.20
		TIME	**-0.08**	**-2.91**	**0.006**
4	AIC: 4.72 ΔAIC: 0.28 wi: 0.08	CV	-0.06	-1.84	0.07
		Total-N	-0.008	-0.27	0.78
		H40	0.03	1.03	0.30
		TIME	**-0.07**	**-2.22**	**0.03**
5	AIC: 4.77 ΔAIC: 0.33 wi: 0.07	**CV**	**-0.07**	**-2.04**	**0.04**
		Total-P	0.01	0.35	0.72
		H30	0.04	1.22	0.22
		TIME	**-0.08**	**-2.88**	**0.006**
6	AIC: 4.78 ΔAIC: 0.34	CV	-0.06	-1.75	0.08
		Total-N	-0.009	-0.31	0.75

	wi: 0.07	H20	0.03	0.94	0.35
		TIME	**-0.07**	**-2.16**	**0.03**
7	AIC: 4.81 ΔAIC: 0.37 wi: 0.07	**CV**	**-0.07**	**-2.06**	**0.04**
		Total-P	0.01	0.41	0.68
		H40	0.04	1.23	0.22
		TIME	**-0.08**	**-2.87**	**0.006**
8	AIC: 4.86 ΔAIC: 0.42 wi: 0.07	CV	-0.06	-1.83	0.07
		Total-N	-0.009	-0.30	0.76
		H50	0.03	1.00	0.32
		TIME	**-0.07**	**-2.20**	**0.03**
9	AIC: 4.94 ΔAIC: 0.50 wi: 0.07	**CV**	**-0.07**	**-2.04**	**0.04**
		Total-P	0.01	0.42	0.67
		H50	0.04	1.20	0.23
		TIME	**-0.07**	**2.85**	**0.007**
10	AIC: 5.00 ΔAIC: 0.56 wi: 0.06	**CV**	**-0.07**	**-1.95**	**0.05**
		Total-P	0.008	0.30	0.76
		H20	0.04	1.11	0.27
		TIME	**-0.08**	**-2.83**	**0.007**
11	AIC: 6.00 ΔAIC: 1.56 wi: 0.04	CV	0.007	0.26	0.79
		Total-P	-0.005	-0.16	0.87
		H20	-0.02	-0.95	0.34
		TIME	-0.04	-1.27	0.21

Functional Richness (FRic) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 469.07 ΔAIC: 0 wi: 0.43	CV	-5445.10	-14.00	0.17
		Total-N	-3394.66	-0.93	0.35
		NDF	102.35	0.31	0.75
		DF	-130.44	-0.21	0.83
		NDF/DF	381.84	0.60	0.54
		TIME	566.93	14.80	0.14
2	AIC: 470.18 ΔAIC: 1.11 wi: 0.24	CV	-5951.89	-14.76	0.14
		Total-P	222.93	0.06	0.94
		NDF	-0.63	-0.01	0.98
		DF	-189.21	-0.30	0.75
		NDF/DF	401.12	0.62	0.53
		TIME	358.39	11.30	0.26
3	AIC: 470.61 ΔAIC: 1.54 wi: 0.20	EH	-2614.78	-0.69	0.48
		Total-N	-414.35	-11.22	0.27
		NDF	-22.62	-0.06	0.95
		DF	-20.70	-0.33	0.75
		NDF/DF	12.58	0.20	0.83
		TIME	**78.00**	**19.33**	**0.05**

Functional Divergence (FDiv) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: -137.95 ΔAIC: 0 wi: 0.05	CV	<0.001	0.20	0.84
		Total-P	0.002	0.72	0.57
		H20	-0.002	-0.55	0.47
		TIME	-0.001	-0.51	0.60
2	AIC: -137.84 ΔAIC: 0.10 wi: 0.05	CV	<0.001	0.13	0.89
		Total-P	0.002	0.72	0.47
		H30	-0.002	-0.48	0.63
		TIME	-0.001	-0.54	0.58
3	AIC: -137.65 ΔAIC: 0.29 wi: 0.05	CV	0.002	0.46	0.64
		Total-N	<0.001	-0.05	0.95
		H20	-0.003	-0.76	0.44
		TIME	-0.001	-0.45	0.65
4	AIC: -137.61 ΔAIC: 0.33 wi: 0.04	CV	<-0.001	-0.03	0.97
		Total-P	0.002	0.77	0.44
		H40	-0.001	-0.25	0.79
		TIME	-0.002	-0.67	0.50
5	AIC: -137.61 ΔAIC: 0.33 wi: 0.04	CV	<-0.001	-0.02	0.98
		Total-P	0.002	0.83	0.40
		H10	-0.001	-0.28	0.77
		TIME	-0.002	-0.61	0.54
6	AIC: -137.60 ΔAIC: 0.34 wi: 0.04	EH	0.001	0.37	0.71
		Total-P	0.003	0.90	0.37
		H20	-0.002	-0.69	0.48
		TIME	-0.002	-0.71	0.47
7	AIC: -137.53 ΔAIC: 0.41 wi: 0.04	CV	<-0.001	-0.10	0.91
		Total-P	0.002	0.79	0.43
		H50	<-0.001	-0.16	0.86
		TIME	-0.002	-0.70	0.48
8	AIC: -137.52 ΔAIC: 0.43 wi: 0.04	CV	0.001	0.40	0.68
		Total-N	<-0.001	-0.03	0.97
		H30	-0.003	-0.70	0.48
		TIME	-0.002	-0.48	0.62
9	AIC: -137.50 ΔAIC: 0.45 wi: 0.04	EH	0.001	0.32	0.74
		Total-P	0.002	0.88	0.38
		H30	-0.002	-0.63	0.53
		TIME	-0.002	-0.70	0.48
10	AIC: -137.35 ΔAIC: 0.59 wi: 0.04	EH	0.001	0.28	0.77
		Total-P	0.003	0.91	0.36
		H10	-0.001	-0.48	0.62
		TIME	-0.002	-0.70	0.48
11	AIC: -137.28 ΔAIC: 0.66 wi: 0.04	EH	<0.001	0.25	0.79
		Total-P	0.002	0.85	0.39
		H40	-0.001	-0.45	0.65

		TIME	-0.002	-0.74	0.46
12	AIC: -137.22 ΔAIC: 0.72 wi: 0.04	EH	<0.001	0.23	0.81
		Total-P	0.002	0.84	0.40
		H50	-0.001	-0.38	0.70
		TIME	-0.002	-0.74	0.46
13	AIC: -137.21 ΔAIC: 0.73 wi: 0.04	CV	0.001	0.25	0.80
		Total-N	<0.001	0.001	0.99
		H40	-0.002	-0.51	0.60
		TIME	-0.002	-0.61	0.54
14	AIC: -137.16 ΔAIC: 0.78 wi: 0.03	CV	<0.001	0.19	0.85
		Total-N	<0.001	0.05	0.95
		H10	-0.001	-0.42	0.67
		TIME	-0.002	-0.62	0.53
15	AIC: -137.07 ΔAIC: 0.87 wi: 0.03	CV	<0.001	0.18	0.85
		Total-N	<0.001	0.02	0.97
		H50	-0.001	-0.44	0.65
		TIME	-0.002	-0.66	0.51
16	AIC: -137.04 ΔAIC: 0.90 wi: 0.03	EH	<0.001	0.11	0.90
		Total-P	0.002	0.78	0.43
		ALK	<0.001	0.19	0.84
		TIME	-0.002	-0.77	0.44
17	AIC: -136.99 ΔAIC: 0.95 wi: 0.03	EH	<0.001	0.16	0.86
		Total-N	<0.001	0.12	0.90
		H20	-0.002	-0.64	0.52
		TIME	-0.003	-0.79	0.42
18	AIC: -136.96 ΔAIC: 0.98 wi: 0.03	CV	<0.001	-0.33	0.73
		Total-P	0.002	0.82	0.41
		ALK	<0.001	0.24	0.80
		TIME	-0.002	-0.82	0.41
19	AIC: -136.93 ΔAIC: 1.01 wi: 0.03	EH	<0.001	0.13	0.89
		Total-N	<0.001	0.11	0.90
		H30	-0.002	-0.60	0.54
		TIME	-0.003	-0.78	0.43
20	AIC: -136.76 ΔAIC: 1.18 wi: 0.03	EH	<0.001	0.13	0.89
		Total-N	<0.001	0.11	0.90
		H30	-0.002	-0.60	0.54
		TIME	-0.003	-0.78	0.43
21	AIC: -136.73 ΔAIC: 1.21 wi: 0.03	EH	<0.001	0.08	0.93
		Total-N	<0.001	0.10	0.92
		H40	-0.001	-0.47	0.63
		TIME	-0.003	-0.79	0.43
22	AIC: -136.72 ΔAIC: 1.22 wi: 0.03	EH	<0.001	0.06	0.94
		Total-N	<0.001	0.12	0.90
		H10	-0.001	-0.40	0.68
		TIME	-0.003	-0.79	0.43
23	AIC: -136.59 ΔAIC: 1.35	EH	<-0.001	-0.07	0.94
		Total-N	<0.001	0.03	0.97

	wi: 0.02	ALK	0.001	0.40	0.68
		TIME	-0.003	-0.79	0.43
24	AIC: -136.49 ΔAIC: 1.45 wi: 0.02	CV	<-0.001	-0.20	0.83
		Total-P	<0.001	0.07	0.93
		ALK	0.001	0.43	0.66
		TIME	-0.003	-0.94	0.35

Functional Dispersion (FDis) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 18.26 ΔAIC: 0 wi: 0.11	CV	-0.06	-137.09	0.14
		Total-P	0.02	0.83	0.40
		H20	**0.09**	**2.09**	**0.04**
		TIME	**-0.10**	**-2.98**	**0.05**
2	AIC: 18.45 ΔAIC: 0.19 wi: 0.10	CV	-0.05	-1.25	0.21
		Total-P	0.02	0.65	0.51
		H10	**0.09**	**2.07**	**0.04**
		TIME	**-0.10**	**-2.99**	**0.005**
3	AIC: 18.63 ΔAIC: 0.37 wi: 0.09	CV	-0.04	1.03	0.30
		Total-N	-0.003	-0.08	0.92
		H10	0.08	1.89	0.06
		TIME	**-0.10**	**-2.50**	**0.01**
4	AIC: 18.74 ΔAIC: 0.48 wi: 0.08	CV	-0.05	-1.07	0.29
		Total-N	-0.001	-0.03	0.97
		H20	0.08	1.84	0.07
		TIME	**-0.10**	**-2.47**	**0.01**
5	AIC: 19.07 ΔAIC: 0.81 wi: 0.07	CV	-0.05	-1.18	0.24
		Total-P	0.02	0.80	0.42
		H30	0.08	1.87	0.07
		TIME	**-0.10**	**-2.87**	**0.007**
6	AIC: 19.51 ΔAIC: 1.25 wi: 0.05	CV	-0.04	-0.87	0.38
		Total-N	-0.004	-0.10	0.91
		H30	0.07	1.61	0.11
		TIME	**-0.10**	**-2.34**	**0.02**
7	AIC: 20.08 ΔAIC: 1.82 wi: 0.04	EH	-0.002	-0.05	0.95
		Total-N	-0.01	-0.41	0.68
		H10	0.05	1.54	0.13
		TIME	**-0.08**	**-2.05**	**0.04**
8	AIC: 20.08 ΔAIC: 1.82 wi: 0.04	CV	-0.04	-0.91	0.36
		Total-P	0.02	0.80	0.42
		H50	0.07	1.58	0.12
		TIME	**-0.09**	**-2.67**	**0.01**
9	AIC: 20.17 ΔAIC: 1.91 wi: 0.04	CV	-0.04	-0.91	0.36
		Total-P	0.02	0.76	0.44
		H40	0.07	1.54	0.13

	TIME	**-0.09**	**-2.66**	**0.01**

Rao's quadratic Entropy GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 185.21 ΔAIC: 0 wi: 0.10	CV	-0.82	-151.00	0.14
		Total-P	0.22	0.58	0.56
		H20	**1.13**	**2.09**	**0.04**
		TIME	**-0.98**	**-2.42**	**0.02**
2	AIC: 185.25 ΔAIC: 0.04 wi: 0.10	CV	-0.66	-1.22	0.22
		Total-N	-0.12	-0.28	0.77
		H20	1.00	1.85	0.07
		TIME	-0.93	-1.86	0.07
3	AIC: 185.47 ΔAIC: 0.26 wi: 0.09	CV	-0.58	-1.13	0.26
		Total-N	-0.15	-0.35	0.72
		H10	0.94	1.81	0.07
		TIME	-0.91	-1.83	0.07
4	AIC: 185.70 ΔAIC: 0.48 wi: 0.08	CV	-0.69	-1.34	0.18
		Total-P	0.14	0.37	0.70
		H10	1.02	1.98	0.05
		TIME	-0.99	-2.39	0.02
5	AIC: 186.07 ΔAIC: 0.85 wi: 0.06	CV	-0.54	-1.02	0.31
		Total-N	-0.15	-0.35	0.72
		H30	0.86	1.61	0.11
		TIME	-0.87	-1.73	0.09
6	AIC: 186.09 ΔAIC: 0.88 wi: 0.06	CV	-0.71	-1.31	0.19
		Total-P	0.22	0.54	0.58
		H30	1.00	1.85	0.07
		TIME	**-0.95**	**-2.31**	**0.02**
7	AIC: 187.12 ΔAIC: 1.91 wi: 0.04	EH	-0.005	-0.01	0.98
		Total-N	-0.30	-0.70	0.48
		H10	0.53	1.34	0.18
		TIME	-0.63	-1.32	0.19
8	AIC: 187.19 ΔAIC: 1.97 wi: 0.03	EH	-0.02	-0.05	0.95
		Total-N	-0.30	-0.69	0.48
		H20	0.52	1.30	0.19
		TIME	-0.61	-1.27	0.21
9	AIC: 187.20 ΔAIC: 1.99 wi: 0.03	CV	-0.37	-0.71	0.48
		Total-N	-0.14	-0.40	0.68
		H40	0.64	1.22	0.23
		TIME	-0.75	-1.50	0.14

General Linear Models of the PARANÁ SUBSYSTEM

Functional BetaSIM GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 14.00 ΔAIC: 0 wi: 0.06	EH	-0.03	-0.92	0.36
		Total-P	0.04	1.29	0.20
		H10	-0.02	-0.67	0.50
		TIME	0.008	0.29	0.77
2	AIC: 14.10 ΔAIC: 0.11 wi: 0.06	EH	-0.03	-0.83	0.40
		Total-P	0.04	1.28	0.20
		ALK	0.02	0.66	0.51
		TIME	-0.002	-0.07	0.93
3	AIC: 14.20 ΔAIC: 0.18 wi: 0.06	EH	-0.03	-0.88	0.38
		Total-P	0.04	-1.31	0.19
		H20	-0.01	-0.55	0.58
		TIME	0.007	0.24	0.81
4	AIC: 14.40 ΔAIC: 0.36 wi: 0.05	EH	-0.03	-0.83	0.41
		Total-P	0.04	1.31	0.19
		H30	-0.01	-0.38	0.70
		TIME	0.005	0.19	0.84
5	AIC: 14.50 ΔAIC: 0.52 wi: 0.05	EH	0.02	-0.74	0.46
		Total-P	0.03	1.34	0.18
		H50	0.03	0.11	0.91
		TIME	0.03	0.07	0.94
6	AIC: 14.50 ΔAIC: 0.53 wi: 0.05	EH	0.03	-0.78	0.44
		Total-P	0.03	1.32	0.19
		H40	0.03	-0.11	0.91
		TIME	0.03	0.11	0.90
7	AIC: 14.60 ΔAIC: 0.64 wi: 0.04	CV	-0.008	-0.27	0.78
		Total-N	-0.03	-0.79	0.43
		H10	-0.02	-0.82	0.41
		TIME	0.02	0.54	0.59
8	AIC: 14.70 ΔAIC: 0.72 wi: 0.04	EH	-0.002	-0.06	0.95
		Total-N	-0.03	-0.73	0.47
		H10	-0.03	-0.97	0.33
		TIME	0.02	0.59	0.56
9	AIC: 14.90 ΔAIC: 0.87 wi: 0.04	CV	0.007	0.21	0.83
		Total-P	0.03	0.93	0.36
		H10	-0.01	-0.49	0.62
		TIME	0.003	0.12	0.90
10	AIC: 14.90 ΔAIC: 0.94 wi: 0.04	CV	0.001	0.05	0.95
		Total-P	0.02	0.88	0.38
		ALK	0.01	0.57	0.56
		TIME	-0.006	-0.19	0.84
11	AIC: 15.00 ΔAIC: 1.02	CV	0.03	-0.37	0.71
		Total-N	0.04	-0.69	0.49

	wi: 0.03	H20	0.03	-0.63	0.53
		TIME	0.04	0.41	0.68
12	AIC: 15.00 ΔAIC: 1.03 wi: 0.03	CV	0.005	0.16	0.87
		Total-P	0.03	0.94	0.35
		H20	-0.01	-0.38	0.70
		TIME	0.001	0.06	0.94
13	AIC: 15.10 ΔAIC: 1.13 wi: 0.03	CV	0.004	0.11	0.90
		Total-P	0.03	0.95	0.34
		H30	-0.007	-0.24	0.80
		TIME	<0.001	0.03	0.97
14	AIC: 15.10 ΔAIC: 1.14 wi: 0.03	EH	<0.001	0.00	0.99
		Total-N	-0.02	-0.62	0.53
		H20	-0.02	-0.76	0.45
		TIME	0.01	0.45	0.65
15	AIC: 15.20 ΔAIC: 1.17 wi: 0.03	CV	<0.001	0.00	0.99
		Total-P	0.03	0.98	0.33
		H50	0.007	0.23	0.81
		TIME	-0.003	-0.10	0.91
16	AIC: 15.20 ΔAIC: 1.20 wi: 0.03	CV	-0.01	-0.52	0.60
		Total-N	-0.01	-0.46	0.64
		ALK	0.02	0.66	0.51
		TIME	<0.001	-0.006	0.99
17	AIC: 15.20 ΔAIC: 1.23 wi: 0.03	CV	0.001	0.05	0.96
		Total-P	0.03	0.97	0.34
		H40	<0.001	0.01	0.99
		TIME	-0.001	-0.05	0.96
18	AIC: 15.20 ΔAIC: 1.23 wi: 0.03	CV	-0.01	-0.44	0.66
		Total-N	-0.02	-0.63	0.53
		H30	-0.01	-0.48	0.63
		TIME	0.01	0.34	0.73
19	AIC: 15.40 ΔAIC: 1.37 wi: 0.03	EH	<0.001	0.01	0.98
		Total-N	-0.01	-0.32	0.75
		ALK	0.02	0.70	0.48
		TIME	-0.001	-0.02	0.97
20	AIC: 15.40 ΔAIC: 1.40 wi: 0.03	EH	0.001	0.06	0.95
		Total-N	-0.02	-0.56	0.57
		H30	-0.01	-0.60	0.55
		TIME	0.01	0.38	0.70
21	AIC: 15.50 ΔAIC: 1.47 wi: 0.03	CV	-0.01	-0.53	0.60
		Total-N	-0.02	-0.55	0.58
		H40	-0.006	-0.21	0.83
		TIME	0.009	0.22	0.82
22	AIC: 15.50 ΔAIC: 1.51 wi: 0.03	CV	-0.01	-0.58	0.56
		Total-N	-0.02	-0.49	0.62
		H50	<0.001	0.01	0.99
		TIME	0.005	0.14	0.88

23	AIC: 15.70 ΔAIC: 1.70 wi: 0.02	EH	0.003	0.12	0.90
		Total-N	-0.02	-0.48	0.63
		H40	-0.01	-0.32	0.75
		TIME	0.01	0.26	0.79
24	AIC: 15.80 ΔAIC: 1.78 wi: 0.02	EH	0.004	0.15	0.88
		Total-N	-0.01	-0.43	0.67
		H50	-0.003	-0.11	0.91
		TIME	0.008	0.19	0.84

Functional BetaSOR GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 12.46 ΔAIC: 0 wi: 0.08	CV	0.06	1.73	0.09
		Total-P	**0.06**	**2.06**	**0.04**
		H10	-0.007	-0.25	0.80
		TIME	-0.02	-0.66	0.51
2	AIC: 12.57 ΔAIC: 0.10 wi: 0.07	CV	0.05	1.73	0.09
		Total-P	**0.06**	**2.07**	**0.04**
		H30	-0.005	-0.18	0.85
		TIME	-0.02	-0.70	0.49
3	AIC: 12.58 ΔAIC: 0.11 wi: 0.07	CV	0.05	1.69	0.09
		Total-P	**0.06**	**2.07**	**0.04**
		H20	-0.002	-0.09	0.93
		TIME	-0.02	-0.73	0.47
4	AIC: 12.59 ΔAIC: 0.12 wi: 0.07	CV	0.05	1.74	0.08
		Total-P	**0.06**	**2.10**	**0.04**
		ALK	-0.009	-0.31	0.75
		TIME	-0.02	-0.67	0.50
5	AIC: 12.60 ΔAIC: 0.13 wi: 0.07	CV	0.05	1.75	0.08
		Total-P	**0.06**	**2.06**	**0.04**
		H40	-0.006	-0.20	0.83
		TIME	-0.02	-0.71	0.48
6	AIC: 12.62 ΔAIC: 0.16 wi: 0.07	CV	0.05	1.73	0.09
		Total-P	**0.06**	**2.07**	**0.04**
		H50	-0.003	-0.13	0.89
		TIME	-0.02	-0.73	0.47
7	AIC: 12.80 ΔAIC: 0.33 wi: 0.06	EH	-0.05	-1.59	0.12
		Total-P	**0.07**	**2.08**	**0.04**
		H10	-0.001	-0.06	0.94
		TIME	-0.02	-0.81	0.42
8	AIC: 12.84 ΔAIC: 0.38 wi: 0.06	EH	-0.05	-1.57	0.12
		Total-P	**0.07**	**2.09**	**0.04**
		H20	0.001	0.04	0.96
		TIME	-0.02	-0.85	0.40
9	AIC: 12.86 ΔAIC: 0.40	EH	-0.05	-1.61	0.11
		Total-P	**0.07**	**2.08**	**0.04**

	wi: 0.06	H30	-0.001	-0.04	0.96
		TIME	-0.02	-0.83	0.41
10	AIC: 12.88 ΔAIC: 0.42 wi: 0.06	EH	-0.05	-1.60	0.11
		Total-P	**0.07**	**2.09**	**0.04**
		ALK	-0.004	-0.15	0.87
		TIME	-0.02	-0.80	0.42
11	AIC: 12.89 ΔAIC: 0.43 wi: 0.06	EH	-0.05	-1.61	0.11
		Total-P	**0.07**	**2.08**	**0.04**
		H50	<-0.001	-0.01	0.99
		TIME	-0.02	-0.85	0.40
12	AIC: 12.90 ΔAIC: 0.43 wi: 0.06	EH	-0.05	-1.62	0.11
		Total-P	**0.07**	**2.08**	**0.04**
		H40	-0.002	-0.07	0.94
		TIME	-0.02	-0.83	0.41

Functional Richness (FRic) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 488.10 ΔAIC: 0 wi: 0.43	CV	66.62	1.47	0.15
		Total-P	-65.79	-1.40	0.17
		NDF	59.63	1.33	0.19
		DF	73.35	0.91	0.36
		NDF/DF	-126.69	-1.56	0.13
		TIME	**150.74**	**3.60**	**0.001**
2	AIC: 489.14 ΔAIC: 1.04 wi: 0.25	**CV**	**89.66**	**2.12**	**0.04**
		Total-N	-41.15	-0.72	0.47
		NDF	46.74	1.05	0.30
		DF	76.59	0.93	0.35
		NDF/DF	-135.00	-1.60	0.12
		TIME	**182.85**	**3.15**	**0.003**
3	AIC: 489.51 ΔAIC: 1.41 wi: 0.21	EH	-36.76	-0.74	0.46
		Total-P	-75.03	-1.46	0.15
		NDF	58.85	1.28	0.21
		DF	69.94	0.85	0.40
		NDF/DF	-117.29	-1.41	0.16
		TIME	**142.39**	**3.35**	**0.002**

Functional Divergence (FDiv) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: -158.17 ΔAIC: 0 wi: 0.08	EH	-0.001	-0.47	0.64
		Total-N	0.005	1.61	0.11
		H10	-0.002	-0.78	0.43

		TIME	**-0.01**	**-3.67**	**<0.001**
2	AIC: -158.09 ΔAIC: 0.08 wi: 0.08	EH	-0.001	-0.46	0.65
		Total-N	0.005	1.70	0.09
		H20	-0.002	-0.78	0.44
		TIME	**-0.01**	**-3.85**	**<0.001**
3	AIC: -158.00 ΔAIC: 0.17 wi: 0.07	CV	<0.001	0.20	0.84
		Total-N	0.005	1.55	0.13
		H10	-0.002	-0.72	0.48
		TIME	**-0.01**	**-3.58**	**0.001**
4	AIC: -157.89 ΔAIC: 0.27 wi: 0.07	CV	<0.001	0.16	0.87
		Total-N	0.005	1.64	0.11
		H20	-0.001	-0.71	0.48
		TIME	**-0.01**	**-3.78**	**<0.001**
5	AIC: -157.82 ΔAIC: 0.34 wi: 0.07	EH	-0.001	-0.40	0.69
		Total-N	0.005	1.76	0.08
		H30	-0.001	-0.61	0.54
		TIME	**-0.01**	**-3.92**	**<0.001**
6	AIC: -157.65 ΔAIC: 0.52 wi: 0.06	CV	<0.001	0.10	0.92
		Total-N	0.005	1.71	0.09
		H30	-0.001	-0.55	0.58
		TIME	**-0.01**	**-3.87**	**<0.001**
7	AIC: -157.61 ΔAIC: 0.56 wi: 0.06	EH	<-0.001	-0.36	0.72
		Total-N	0.006	1.82	0.07
		H40	-0.001	-0.46	0.65
		TIME	**-0.01**	**-4.07**	**<0.001**
8	AIC: -157.60 ΔAIC: 0.57 wi: 0.06	EH	-0.08	-2.70	0.01
		Total-N	0.08	2.10	0.04
		ALK	-0.02	-0.88	0.38
		TIME	**-0.11**	**-2.84**	**0.007**
9	AIC: -157.54 ΔAIC: 0.63 wi: 0.06	EH	<-0.001	-0.34	0.73
		Total-N	0.006	1.84	0.07
		H50	<-0.001	-0.36	0.72
		TIME	**-0.01**	**-4.08**	**<0.001**
10	AIC: -157.45 ΔAIC: 0.71 wi: 0.05	CV	<0.001	0.04	0.96
		Total-N	0.005	1.78	0.08
		H40	-0.001	-0.40	0.69
		TIME	**-0.01**	**-4.03**	**<0.001**
11	AIC: -157.39 ΔAIC: 0.78 wi: 0.05	CV	<0.001	0.02	0.98
		Total-N	0.005	1.79	0.08
		H50	<-0.001	-0.30	0.76
		TIME	**-0.01**	**-4.05**	**<0.001**
12	AIC: -157.35 ΔAIC: 0.82 wi: 0.05	CV	0.05	1.69	0.09
		Total-N	0.06	1.60	0.11
		ALK	-0.02	-0.81	0.41
		TIME	**-0.10**	**-2.56**	**0.01**

Functional Dispersion (FDis) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 17.58 ΔAIC: 0 wi: 0.08	EH	-0.06	-1.81	0.07
		Total-N	**0.08**	**2.00**	**0.05**
		H50	0.02	0.65	0.51
		TIME	**-0.13**	**-3.10**	**0.003**
2	AIC: 17.70 ΔAIC: 0.11 wi: 0.07	EH	-0.05	-1.75	0.08
		Total-N	0.07	1.79	0.08
		ALK	-0.01	-0.60	0.54
		TIME	**-0.11**	**-2.78**	**0.008**
3	AIC: 17.85 ΔAIC: 0.26 wi: 0.07	EH	-0.06	-1.89	0.06
		Total-N	0.07	1.74	0.09
		H10	-0.002	-0.08	0.93
		TIME	**-0.12**	**-2.68**	**0.01**
4	AIC: 17.87 ΔAIC: 0.29 wi: 0.07	EH	-0.06	-1.85	0.07
		Total-N	0.08	1.92	0.06
		H40	0.01	0.38	0.70
		TIME	**-0.12**	**-3.00**	**0.005**
5	AIC: 17.93 ΔAIC: 0.34 wi: 0.07	EH	-0.06	-1.86	0.07
		Total-N	0.08	1.87	0.07
		H30	0.006	0.20	0.84
		TIME	**-0.12**	**-2.89**	**0.006**
6	AIC: 17.93 ΔAIC: 0.35 wi: 0.06	EH	-0.06	-1.89	0.06
		Total-N	0.08	1.79	0.08
		H20	0.001	-0.05	0.96
		TIME	**-0.12**	**-2.78**	**0.008**
7	AIC: 18.02 ΔAIC: 0.43 wi: 0.05	CV	0.05	1.69	0.09
		Total-N	0.06	1.59	0.11
		H50	-0.02	-0.82	0.41
		TIME	**-0.10**	**-2.55**	**0.01**
8	AIC: 18.28 ΔAIC: 0.69 wi: 0.05	CV	0.05	1.60	0.11
		Total-N	0.07	1.74	0.09
		H50	0.01	0.54	0.59
		TIME	**-0.12**	**-2.82**	**0.008**
9	AIC: 18.30 ΔAIC: 0.71 wi: 0.05	CV	0.06	1.75	0.08
		Total-N	0.06	1.43	0.16
		H10	-0.01	-0.27	0.78
		TIME	**-0.10**	**-2.32**	**0.02**
10	AIC: 18.45 ΔAIC: 0.86 wi: 0.05	CV	0.05	1.74	0.09
		Total-N	0.06	1.51	0.14
		H20	-0.006	-0.18	0.86
		TIME	**-0.11**	**-2.47**	**0.01**
11	AIC: 18.51 ΔAIC: 0.92 wi: 0.05	CV	0.05	1.66	0.10
		Total-N	0.07	1.66	0.10
		H40	0.008	0.25	0.80

		TIME	**-0.11**	**-2.71**	**0.01**
12	AIC: 18.51 ΔAIC: 0.93 wi: 0.05	CV	0.05	1.69	0.10
		Total-N	0.06	1.60	0.11
		H30	0.002	0.06	0.95
		TIME	**-0.11**	**-2.58**	**0.01**

Rao's quadratic Entropy GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 187.58 ΔAIC: 0 wi: 0.07	**EH**	**-1.00**	**-2.63**	**0.01**
		Total-N	**0.95**	**1.95**	**0.05**
		ALK	-0.35	-0.96	0.34
		TIME	**-1.20**	**-2.52**	**0.01**
2	AIC: 187.66 ΔAIC: 0.08 wi: 0.07	EH	-0.76	-1.89	0.06
		Total-N	1.01	1.89	0.06
		H50	0.22	0.56	0.57
		TIME	**-1.47**	**-2.82**	**0.007**
3	AIC: 187.82 ΔAIC: 0.24 wi: 0.06	**EH**	**-0.81**	**-1.96**	**0.05**
		Total-N	0.92	-1.66	0.10
		H10	-0.03	-0.07	0.94
		TIME	**-1.35**	**-2.46**	**0.01**
4	AIC: 187.87 ΔAIC: 0.29 wi: 0.06	CV	0.68	1.76	0.08
		Total-N	0.75	1.50	0.14
		ALK	-0.34	-0.89	0.37
		TIME	**-1.14**	**-2.28**	**0.02**
5	AIC: 187.88 ΔAIC: 0.29 wi: 0.06	EH	-0.78	-1.92	0.06
		Total-N	0.99	1.83	0.07
		H40	0.13	0.33	0.74
		TIME	**-1.43**	**-2.74**	**0.009**
6	AIC: 187.90 ΔAIC: 0.32 wi: 0.06	**EH**	**-0.79**	**-1.93**	**0.05**
		Total-N	**0.97**	**1.78**	**0.05**
		H30	0.08	0.18	0.62
		TIME	**-1.41**	**-2.65**	**0.008**
7	AIC: 187.90 ΔAIC: 0.32 wi: 0.06	**EH**	**-0.81**	**-1.95**	**0.05**
		Total-N	0.94	1.72	0.09
		H20	0.00	-0.01	0.99
		TIME	**-1.37**	**-2.56**	**0.01**
8	AIC: 188.29 ΔAIC: 0.70 wi: 0.05	CV	0.76	1.82	0.07
		Total-N	0.73	1.34	0.19
		H10	-0.12	-0.27	0.79
		TIME	**-1.17**	**-2.09**	**0.04**
9	AIC: 188.35 ΔAIC: 0.77 wi: 0.05	CV	0.68	1.68	0.10
		Total-N	0.85	1.62	0.11
		H50	0.18	0.44	0.66
		TIME	**-1.33**	**-2.53**	**0.01**

10	AIC: 188.44 ΔAIC: 0.86 wi: 0.05	CV	0.74	1.80	0.08
		Total-N	0.76	1.43	0.16
		H20	-0.06	-0.14	0.88
		TIME	**-1.21**	**-2.24**	**0.03**
11	AIC: 188.50 ΔAIC: 0.92 wi: 0.04	CV	0.72	1.76	0.08
		Total-N	0.79	1.49	0.14
		H30	0.02	0.04	0.96
		TIME	**-1.26**	**-2.33**	**0.02**
12	AIC: 188.52 ΔAIC: 0.94 wi: 0.04	CV	0.70	1.74	0.09
		Total-N	0.81	1.55	0.13
		H40	0.08	0.19	0.84
		TIME	**-1.28**	**-2.44**	**0.01**

General Linear Models of the IVINHEMA SUBSYSTEM

Functional BetaSIM GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 7.8 ΔAIC: 0 wi: 0.10	**CV**	**0.06**	**2.329**	**0.02**
		Total-P	0.006	0.24	0.81
		H50	-0.03	-1.294	0.20
		TIME	-0.01	-0.39	0.70
2	AIC: 7.8 ΔAIC: 0.05 wi: 0.09	**CV**	**0.06**	**2.388**	**0.02**
		Total-N	-0.005	-0.19	0.84
		H50	-0.03	-1.352	0.18
		TIME	-0.01	-0.44	0.66
3	AIC: 7.8 ΔAIC: 0.06 wi: 0.09	**CV**	**0.06**	**2.302**	**0.02**
		Total-P	0.009	0.32	0.74
		H40	-0.03	-1.277	0.21
		TIME	-0.01	-0.37	0.70
4	AIC: 7.9 ΔAIC: 0.17 wi: 0.09	**CV**	**0.06**	**2.359**	**0.02**
		Total-N	-0.004	-0.16	0.86
		H40	-0.03	-1.311	0.19
		TIME	-0.01	-0.46	0.64
5	AIC: 8.2 ΔAIC: 0.38 wi: 0.08	**CV**	**0.06**	**2.242**	**0.03**
		Total-P	0.01	0.43	0.66
		H30	-0.03	-1.136	0.26
		TIME	-0.009	-0.32	0.74
6	AIC: 8.4 ΔAIC: 0.58 wi: 0.07	**CV**	**0.06**	**2.291**	**0.02**
		Total-N	-0.003	-0.10	0.91
		H30	-0.03	-1.131	0.26
		TIME	-0.01	-0.45	0.65
7	AIC: 8.4 ΔAIC: 0.65 wi: 0.07	**CV**	**0.05**	**2.187**	**0.03**
		Total-P	0.01	0.49	0.62
		H20	-0.02	-1.012	0.31
		TIME	-0.01	-0.35	0.72

8	AIC: 8.7 ΔAIC: 0.94 wi: 0.06	**CV**	**0.06**	**2.227**	**0.03**
		Total-N	-0.001	-0.04	0.96
		H20	-0.02	-0.97	0.33
		TIME	-0.01	-0.51	0.60
9	AIC: 9.1 ΔAIC: 1.36 wi: 0.05	**CV**	**0.05**	**-2.098**	**0.04**
		Total-P	0.01	0.46	0.64
		H10	-0.01	-0.52	0.60
		TIME	-0.01	-0.45	0.65
10	AIC: 9.4 ΔAIC: 1.59 wi: 0.04	**CV**	**0.06**	**2.108**	**0.04**
		Total-N	<0.001	<0.001	0.99
		H10	-0.01	-0.47	0.63
		TIME	-0.01	-0.60	0.54
11	AIC: 9.4 ΔAIC: 1.63 wi: 0.04	**CV**	**0.05**	**2.01**	**0.05**
		Total-P	0.01	0.46	0.64
		ALK	-0.007	-0.27	0.78
		TIME	-0.01	-0.59	0.55
12	AIC: 9.7 ΔAIC: 1.94 wi: 0.03	**CV**	**0.05**	**2.05**	**0.04**
		Total-N	0.002	0.009	0.92
		ALK	-0.004	-0.16	0.86
		TIME	-0.02	-0.77	0.44

Functional BetaSOR GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 11.5 ΔAIC: 0 wi: 0.08	CV	0.02	0.86	0.39
		Total-P	0.05	1.87	0.06
		ALK	0.02	0.86	0.39
		TIME	-0.008	-0.29	0.76
2	AIC: 11.7 ΔAIC: 0.12 wi: 0.08	EH	-0.02	-0.69	0.49
		Total-P	**0.06**	**2.03**	**0.05**
		H10	0.03	0.98	0.33
		TIME	-0.01	-0.43	0.66
3	AIC: 11.7 ΔAIC: 0.15 wi: 0.08	EH	-0.02	-0.70	0.48
		Total-P	**0.06**	**2.28**	**0.02**
		H50	0.03	0.97	0.33
		TIME	-0.009	-0.32	0.75
4	AIC: 11.8 ΔAIC: 0.30 wi: 0.07	CV	0.02	0.70	0.48
		Total-P	**0.06**	**2.03**	**0.05**
		H10	0.01	0.61	0.54
		TIME	-0.01	-0.38	0.70
5	AIC: 11.9 ΔAIC: 0.32 wi: 0.07	EH	-0.02	-0.64	0.52
		Total-P	**0.06**	**2.14**	**0.04**
		H30	0.02	0.88	0.38
		TIME	-0.01	-0.38	0.70
6	AIC: 11.9 ΔAIC: 0.34	EH	-0.02	-0.65	0.52
		Total-P	**0.06**	**2.22**	**0.03**

	wi: 0.07	H40	0.02	0.88	0.38
		TIME	-0.009	-0.32	0.75
7	AIC: 11.9 ΔAIC: 0.37 wi: 0.07	CV	0.01	0.66	0.51
		Total-P	**0.06**	**2.14**	**0.03**
		H50	0.01	0.55	0.58
		TIME	-0.009	-0.31	0.75
8	AIC: 11.9 ΔAIC: 0.41 wi: 0.07	CV	0.02	0.71	0.48
		Total-P	**0.06**	**2.08**	**0.04**
		H30	0.01	0.53	0.59
		TIME	-0.01	-0.34	0.73
9	AIC: 12.00 ΔAIC: 0.45 wi: 0.07	CV	0.02	0.69	0.49
		Total-P	**0.06**	**2.12**	**0.04**
		H40	0.01	0.50	0.62
		TIME	-0.009	-0.31	0.76
10	AIC: 12.10 ΔAIC: 0.56 wi: 0.06	CV	0.02	0.75	0.45
		Total-P	**0.06**	**2.05**	**0.04**
		H20	0.01	0.37	0.71
		TIME	-0.009	-0.30	0.76
11	AIC: 12.20 ΔAIC: 0.63 wi: 0.06	EH	-0.01	-0.56	0.58
		Total-P	**0.06**	**2.08**	**0.04**
		H20	0.02	0.68	0.50
		TIME	-0.01	-0.34	0.73
12	AIC: 12.20 ΔAIC: 0.68 wi: 0.06	EH	-0.007	-0.25	0.79
		Total-P	**0.06**	**2.02**	**0.05**
		ALK	0.02	0.80	0.42
		TIME	-0.008	-0.30	0.76

Functional Richness (FRic) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 192.5 ΔAIC: 0 wi: 0.76	CV	-0.75	-1.77	0.08
		Total-P	0.97	1.69	0.09
		NDF	-0.30	-0.68	0.50
		DF	0.00	0.00	0.99
		NDF/DF	-0.18	-0.22	0.82
		TIME	**-1.47**	**-2.61**	**0.01**
2	AIC: 194.9 ΔAIC: 2.36 wi: 0.23	EH	-0.34	-0.69	0.49
		Total-P	-0.42	-0.82	0.41
		NDF	-0.04	-0.09	0.93
		DF	0.05	**0.05**	0.95
		NDF/DF	-0.40	-0.49	0.63
		TIME	**-0.85**	-1.98	**0.04**

Functional Divergence (FDiv) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 1.56 ΔAIC: 0 wi: 0.09	**CV**	**-0.009**	**-2.38**	**0.02**
		Total-P	0.001	0.38	0.70
		H50	**0.008**	**2.22**	**0.03**
		TIME	**0.005**	**1.30**	**0.20**
2	AIC: 1.56 ΔAIC: 0.01 wi: 0.09	**CV**	**-0.009**	**-2.26**	**0.03**
		Total-N	<0.001	0.06	0.94
		H50	**0.008**	**2.14**	**0.03**
		TIME	**0.004**	**1.23**	**0.22**
3	AIC: 1.56 ΔAIC: 0.07 wi: 0.09	**CV**	**-0.008**	**-2.30**	**0.02**
		Total-P	<0.001	0.22	0.81
		H40	**0.008**	**2.14**	**0.03**
		TIME	**0.005**	**1.28**	**0.20**
4	AIC: 1.56 ΔAIC: 0.08 wi: 0.09	**CV**	**-0.008**	**-2.20**	**0.03**
		Total-N	<0.001	0.01	0.98
		H40	**0.008**	**2.08**	**0.04**
		TIME	**0.004**	**1.26**	**0.21**
5	AIC: 1.56 ΔAIC: 0.08 wi: 0.09	**CV**	**-0.008**	**-220.72**	**0.03**
		Total-P	<0.001	0.05	0.95
		H30	**0.007**	**197.62**	**0.05**
		TIME	0.004	116.66	0.25
6	AIC: 1.55 ΔAIC: 0.47 wi: 0.07	**CV**	**-0.008**	**-2.12**	**0.04**
		Total-N	<-0.001	0.04	0.96
		H30	**0.007**	**1.93**	**0.06**
		TIME	0.004	1.19	0.23
7	AIC: 1.55 ΔAIC: 0.49 wi: 0.07	**CV**	**-0.008**	**-2.07**	**0.04**
		Total-P	<-0.001	-0.05	0.95
		H20	<0.001	1.67	0.10
		TIME	0.005	1.22	0.23
8	AIC: 1.55 ΔAIC: 0.57 wi: 0.07	**CV**	**-0.008**	**-1.99**	**0.05**
		Total-N	<-0.001	-0.15	0.87
		H20	0.006	1.62	0.11
		TIME	0.005	1.29	0.20

Functional Dispersion (FDis) GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 38.13 ΔAIC: 0 wi: 0.09	CV	-0.06	-1.50	0.14
		Total-P	**-0.10**	**-2.20**	**0.03**
		H10	0.07	1.55	0.13
		TIME	**-0.12**	**-2.57**	**0.01**
2	AIC: 39.19 ΔAIC: 1.06 wi: 0.09	CV	-0.06	-1.39	0.17
		Total-P	**-0.09**	**-2.13**	**0.04**
		H20	0.05	1.15	0.26
		TIME	**-0.11**	**-2.41**	**0.02**

3	AIC: 39.30 ΔAIC: 1.16 wi: 0.09	CV	-0.06	-1.41	0.16
		Total-P	**-0.09**	**-2.06**	**0.04**
		H30	0.05	1.09	0.28
		TIME	**-0.11**	**-2.39**	**0.02**
4	AIC: 39.60 ΔAIC: 1.43 wi: 0.08	CV	-0.05	-1.27	0.21
		Total-P	-0.08	-1.79	0.08
		ALK	-0.04	-0.98	0.33
		TIME	**-0.09**	**-2.06**	**0.04**
5	AIC: 39.61 ΔAIC: 1.48 wi: 0.08	CV	-0.06	-1.39	0.17
		Total-P	**-0.08**	**-1.96**	**0.05**
		H40	0.04	0.93	0.35
		TIME	**-0.10**	**-2.32**	**0.02**
6	AIC: 39.73 ΔAIC: 1.60 wi: 0.07	CV	-0.06	-1.39	0.17
		Total-P	-0.09	-1.90	0.06
		H50	0.04	0.85	0.40
		TIME	**-0.10**	**-2.29**	**0.02**

Rao's quadratic Entropy GLS models with ΔAIC<2

	Model	Predictor	Coefficient value (SE)	*t-value*	*P*
1	AIC: 214.98 ΔAIC: 0 wi: 0.12	EH	-0.75	-1.77	0.08
		Total-N	0.97	-1.70	0.09
		NDF	-0.30	-0.68	0.50
		DF	0.00	0.00	0.99
		NDF/DF	-0.18	-0.22	0.82
		TIME	**-1.47**	**-2.61**	**0.01**
2	AIC: 215.45 ΔAIC: 0.46 wi: 0.10	EH	-0.34	-0.69	0.49
		Total-P	-0.42	-0.82	0.41
		NDF	-0.03	-0.09	0.93
		DF	0.04	0.05	0.95
		NDF/DF	-0.40	-0.49	0.63
		TIME	**-0.84**	**-1.98**	**0.04**

CHAPTER 3

ENVIRONMENTAL AND PHYLOGENETIC VARIATION EXPLAINING LONG-TERM PATTERNS OF AQUATIC MACROPHYTES DISTRIBUTION AT DIFFERENT SCALES IN A NEOTROPICAL FLOODPLAIN

Environmental and phylogenetic variation explaining long-term patterns of aquatic macrophytes distribution at different scales in a Neotropical floodplain

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Abstract

Species distribution is determined by a combination of environmental filtering, species ecological interaction, evolutive history and dispersal mechanisms. Here we aim to assess the variation in the taxonomic and phylogenetic structure of aquatic macrophytes communities in a Neotropical floodplain along 11 years considering three different spatial scales (grain size) – floodplain, river and lake in order to respond: does phylogenetic relatedness drives the temporal changes in composition of aquatic macrophyte species along the environmental gradients? We also investigated the relationship between aquatic macrophyte distributions and functional traits. Our results indicated that aquatic macrophytes distributions considering phylogenetic relatedness and community structure are explained by gradients of environmental variables at larger scales. Even so, the clearest pattern was the dependency of distribution according to environmental classification in subsystems (likely ecoregions within the floodplain). Several traits related to aquatic macrophyte distribution, but those related to life forms seems to be the best to indicate how community distribution respond to environmental gradients.

Key words: Environmental gradient, Functional traits, Phylogenetic relatedness, Species distribution, Subsystem classification.

Introduction

Organization of biological communities considering species distribution has been unanimously debated in ecology studies (Guisan & Zimmermann 2000; Austin, 2002, Guisan & Thuiller, 2005; Elith & Graham, 2009). Most likely, a combination of environmental filtering, interspecific interactions (Bascompte, 2009; Wisz et al., 2013), historic biogeography and dispersal shapes species distribution along sites (Vellend, 2010). Environmental filtering acts in ecological communities selecting species with traits that could handle ecosystems conditions. This selection could incorporate species closely related that have similar traits shaping a clustered community structure or; species unrelated with specific traits selected and that will become part of overdispersal community (Grime, 2006; Mayfield & Levine, 2010). Meanwhile, different species response to abiotic environmental changes along environmental gradients may influence the nature of biotic interactions (Brooker, 2006; Meier, Edwards, Kienast, Dobbertin & Zimmermann, 2010). The result of the evolutionary history also shape species distribution among biological assemblages given it determines the regional pool of species that are phylogenetically related (Anderson, Lachance & Starmer, 2004, Weigelt et al., 2015) and are more or less similar considering functional traits (Anderson et al., 2004). Beyond the abovementioned processes, species dispersion is also important for theis distribution along sites (Vellend 2010), and may relate to the main routes of dispersal (Heino, Melo & Bini, 2015). Particularly for aquatic organisms, water flow and connectivity are directly linked to species distribution success (Landeiro, Bini, Melo, Pes & Magnusson, 2012). For instance, vegetative propagules of aquatic macrophytes usually disperse throughout local water courses, whereas sexual propagules can reach longer distances through animal dispersion (Santamaría, 2002).

Floodplains are dynamic aquatic environments composed by rivers, tributaries and lakes connected permanently, or periodically by overflows (Junk, Bayley & Sparks, 1989; Neiff, 1990). Floodplains are model ecosystems to evaluate land and water ecotones (Bayley, 1995). Taking into account the nature of rivers that compose a floodplain, they can be from a similar hydrobasin or not (i.e. the so called “subsystems” hereafter). It is possible that subsystems with distinct abiotic features (e.g., Roberto, Santana & Thomaz, 2009) may also have different evolutionary histories. Extending the rationale, subsystems can also differ from each other considering the community assembly processes within them, such as the environmental filtering. Indeed, a

consequence of different geological histories in floodplains is the high biodiversity (Agostinho, Thomaz, Minte-Vera & Winemiller, 2000) given that communities from distinct river systems usually differ (Padial et al., 2012). At low water levels, spatial heterogeneity enhances subsystems differences, while at flood events, sites become spatially connected allowing exchange of propagules, nutrients, sediments, minerals and organisms (Thomaz, Bini & Bozelli, 2007). Yet, an environmental impact, such as a dam construction upstream the floodplain could unsettle the acting environmental filter and contribute to environmental homogenization and differentiation, such as nutrient dynamic change (Roberto et al., 2009), ecological predictors alteration and the induce of a productivity decrease along the time due to nutrient retentions (Roberto et al., 2009). In such case, community assembly mechanisms among and within subsystems could change over time.

In this study, we assessed the variation in the taxonomic and phylogenetic structure of aquatic macrophytes communities in the Upper Paraná River floodplain (UPRF) along 11 years. This Neotropical floodplain has been severely impacted over time due to dam operations upstream and downstream (Agostinho, Thomaz & Gomes, 2005). Aquatic macrophyte species occurrences were registered in lakes of three different subsystems that assure a major environmental gradient of the floodplain. We evaluated community organization over time at three spatial scales considering the unit grain size: floodplain, subsystem and lake. We investigated whether the phylogenetic relatedness drives the temporal changes in composition of aquatic macrophyte species along the environmental gradients, its relationship with establishment and dispersal traits, and the influence of the spatial scale on it.

Here, we are investigating the variation in taxonomic and phylogenetic diversity over time in three different spatial grains. First, we conducted analysis pooling floodplain scale and hypothesized that species distribution changes over time are driven by environmental variables, irrespective of phylogenetic relationships due to the recent historical event of oligotrophication at the floodplain. Secondly we analyze subsystem scale and hypothesized that species distribution changes over time are driven by environmental variables and phylogenetic relationships due to the different subsystems origins, and likely different community assembly mechanisms. Finally we analyze lake scale and hypothesized that species distribution changes over time can be either driven by environmental variables and phylogenetic relationships. This could be a reflect of the oligotrophication process occurred at the floodplain, and also differences among

subsystems and lakes, since lakes within subsystems were either permanently or temporarily connected to the main river channel. In this case the dominant mechanism can be identified, that is environmental variables or phylogenetic relatedness.

When species distribution are explained by environmental variables or phylogenetic relationships (more than expected by a null model), we also investigated the relationship between species distributions and functional traits related. We did that to explore if some particular trait is a clear consequence of distributional patterns depending on the scale. Given the intense and effective vegetative reproduction noticed for most aquatic macrophytes species (Pott et al. 2011; Touchette et al. 2011), we expect that morphological traits related to the way that species explore resources will be the most related to distributional patterns. In this sense, the simple classification in functional groups (*sensu* Pedralli, 1990) may capture the most important differences in how plants explore resources in habitats.

Material and Methods

Study area

The Upper Paraná River floodplain (UPRF) is located in South Brazil (Agostinho & Zalewski, 1996). As a major floodplain, hydrological regime is characterized by droughts and floods that strike this floodplain in different matters, and it is considered the main driving force of aquatic macrophyte communities (Thomaz, Carvalho, Padial & Kobayashi, 2009). However, Paraná River hydrographic basin has the highest number of dams compared to any other hydrographic basin in South America (Souza-Filho, 2009), and the UPRF is under influence of upstream and downstream reservoirs: the water discharge is controlled according to the upstream dams operation (Souza-Filho, 2009). Therefore, the UPRF had its hydrological regime, flow velocity, sediment transport and bank erosion modified due to dams' construction (Souza-Filho, 2009), and continuous changes have been reported for several abiotic features, such as a continuous decrease in nutrient concentrations and an increase in water transparency (Roberto et al., 2009).

Even so, water level oscillations still determine sites connectivity and abiotic and biotic structures and processes (Thomaz et al., 2007). Beyond the influence of the water levels, the floodplain is composed of three different subsystems (Baia, Paraná, and Ivinhema rivers) also responsible for the major environmental variation of the

UPRF due to their limnological, geomorphological and biological characteristics (Padial et al., 2012).

Data sampling

Aquatic macrophytes occurrences were obtained by a dataset of a Long-Term Ecological Project at the UPRF. Six lakes were sampled in each sampling period: two from each subsystem, in which one was permanently connected and the other temporarily connected to the main river channel. Sampling occurred four times a year (November - February; May - August), representing the beginning and the end of flooding and drought periods respectively, along 11 years (2002-2012). For other details of long-term samplings and sampling periods, see Soares et al. (2015), Dittrich, Dias, Bonecker, Lansac-Tôha & Padial (2016); Ceschin, Bini & Padial (2018). We used 38 periods that had complete data for analyses described below. Along the 38 periods of sampling, 76 aquatic macrophyte taxa, belonging to 54 genera and 35 families were recorded.

Morphological functional traits of species were not measured during the long-term monitoring. Therefore, an intensive sampling was performed at several lakes in November 2015 to estimate traits for most taxa recorded. In this case, five modules were collected from each taxon in order to estimate traits mean value. A module was determined as the minor repeating portion containing a root, stem, and leaves (Pérez-Harguindeguy et al., 2013). This approach was adopted in order to standardize samplings and due to the fact that most taxa have efficient vegetative propagation, making it difficult to separate individuals. For each module, 10 continuous traits were measured and seven categorical traits were obtained from information available in articles and books (Table 1). Only literature traits were obtained for those taxa not found in the intensive sampling (either continuous or categorical). In total, 3.800 continuous traits were measured (5 modules x 76 taxa x 10 continuous traits) and 532 categorical traits were registered (76 taxa x 7 categorical traits). Traits were chosen given they are related to morphology, growth and life form. Indeed, they have been commonly used to describe how environmental conditions affect species reproduction, growth and survival; and how species disperse (Cavalli, Baattrup-Pedersen & Riis, 2014). For aquatic macrophytes a long-term used classification in functional groups is the most popular way to differentiate species accruing to their functional role in habitats. We used the classification proposed by Pedralli (1990) that divided plants in

the following groups: 1) fixed submersed, 2) free submersed, 3) fixed floating, 4) free floating, 5) emergent, 6) amphibious and 7) epiphyte. We also used other morphological traits suggested as important for aquatic macrophytes (Fu, Yuan, et al., 2018) such as leaf pilosity and consistency, stem position, root architecture as well as height, width and length of leaf, stem and root (Table 1).

The following environmental conditions of the UPRF were obtained *in situ* at each lake along the 11 years of the long-term monitoring, and were thus considered environmental gradients that can likely explain aquatic macrophyte distribution: Total-P ($\mu g \cdot L^{-1}$), Total-N ($\mu g \cdot L^{-1}$), temperature (°C), pH, turbidity (NTU), inorganic suspended material ($mg \cdot L^{-1}$) (ISM). The hydrometric level 30 days before the sampling (HL30) was also estimated as a proxy of flood influence. We used these proxies given they were the best according to our models (for more details of variables representing hydrometric levels, see Soares et al., 2015, Ceschin et al., 2017).

Table 1. Chosen functional traits of aquatic macrophytes phylogenetic diversity description. See Supplementary Material 1 for each species traits.

	CLASSIFICATION	TRAITS
OBTAINED FROM LITERATURE	PLANT	*Amphibious*
		Emergent
		Epiphyte
		Fixed floating
		Free floating
		Fixed Submerged
		Free Submerged
		Annual
		Perennial
		Monthly blooming
		Semester blooming
		Annual blooming
	LEAF	*Glabrous pilosity*
		Pilous pilosity
		Coriaceous consistency
		Herbaceous consistency
	STEM	*Erect*
		Prostrate
	ROOT	*Fasciculate*
		Pivoting
MEASURED IN THE LABORATORY	PLANT	*Height (cm)*
	LEAF	*Width (cm)*
		Length (cm)
		Thickness (mm)
	PETIOLE	*Length (mm)*
		Presence/ absence
	STEM	*Thickness (mm)*
		Presence/ absence
	ROOT	*Length (cm)*
		Presence/ absence

Data analysis

- *Phylogenetic structures along environmental gradients*

To estimate the influence of phylogenetic relationships considering species occurrences, we performed an analysis of principal coordinates of phylogenetic structure (PCPS; Duarte, 2011). For this, we first reconstructed a phylogeny for all sampled species (Supplementary Material 2) based on the phylogenetic hypothesis of Smith & Brown (2018), which was reconstructed based on data from GenBank and the Open Tree of Life taxa with a backbone and age estimates provided by Magallón, Gómez-Acevedo, Sánchez-Reyes & Hernández-Hernández (2015) (ALLMB tree file). The PCPS analysis first generates a phylogenetic weighted matrix of taxon composition (matrix **P**), where our sampling units were represented by temporal plots, expressing the representativeness of phylogenetic lineages per plot over the 38 periods sampled. From matrix **P**, a principal coordinate analysis (PCoA) is performed based on square root-transformed Bray-Curtis dissimilarities, obtaining the PCPS eigenvectors describing an orthogonal phylogenetic gradient in the data set. The PCPS eigenvectors with higher eigenvalues describe wide and deep node phylogenetic gradients, while finer taxonomic scales are described as eigenvalues decrease. Therefore, the PCPS enables to explore the lineages association with the temporal gradient (Duarte, Debastiani, Freitas & Pillar, 2016).

In order to assess the effect of the environmental gradient on species distribution along the samplings, the PCPS with at least 5% of total variation on matrix P were related to different environmental models. These models (Supplementary Material 3) were constructed *a priori* based and applied at the three spatial scales of analysis (floodplain, subsystem, and lake). In each model, we included variables representing different processes. At the floodplain scale, PCPSs were modeled including the HL30 and/or limnological variables (representing local abiotic conditions). At the subsystem scale, PCPSs were modeled including variables above and/or a variable identifying the subsystem in which sampling units were located. At the lake scale, PCPSs were modeled including all variables above and/or a variable indicating if the lake is permanently connected or not to the main river channel.

Therefore, several models were generated considering the possible combination of variables (in a model, only uncorrelated predictors were included, i.e., $r < 0.5$), and compared among each other based on the Akaike's Information Criterion (AIC;

Burnham & Anderson, 2002). In all models (at different scales), we also included a variable called "TIME", to control for temporal autocorrelation using an autocorrelation structure of order 1 through a continuous time covariate (corCAR1, see Pinheiro & Bates, 2000). We used this autocorrelation structure given it was the best for our modeling approach considering the AIC. All models were adjusted through (1) ordinary least squares (OLS) models; and generalized least squares (GLS) models. We considered the best models for each PCPS selecting those with a $\Delta AIC \leq 2$ and lower than a null model containing only the intercept.

- *Null models*

To test if the organization of species distribution along the 38 periods of samplings and the environmental variables is mediated or not by phylogenetic relationships, the best-fitted models were tested using two null models. The first null model (*site.shuffle*) shuffles the sampling units along the environmental gradient, while the second null model (*taxa.shuffle*) shuffles the species along the phylogeny, both testing the null model of independence between the environment and species occurrence. If both null models reject the null hypothesis, the association of species distribution over the 11 years and the environmental gradient is mediated by phylogenetic relatedness. If only site shuffle is significant, the association of the environment gradient and species distribution over time is not mediated by phylogeny, *e.g* some species are associated to specific environmental conditions but the whole phylogenetic clade is not organized along the gradient (Duarte et al., 2016).

The PCPS analysis and the null model tests (*site* and *taxa.shuffle; pcps.sig* function) were performed using the PCPS v 1.0.5 package (Debastiani & Duarte, 2014). The GLS models and the model selection based on AIC criterion were performed at the nlme v. 3.1-131 and the MuMIn v. 1.15.6 packages, both in the R Statistical Environment (R Core Team, 2018).

- *Relationship with functional traits*

To evaluate the relationship of plant traits (Table 1) and the temporal species distribution, we first calculated a matrix of community weighted means using species occurrences and traits values tables (CWM; Garnier et al., 2004). CWM expresses the average of trait values in each community, in our case communities were separated by periods. For each trait of CWM, we performed a Pearson correlation with the PCPS that

presented model(s) better than the null model in the model selection procedure (see above). The CWM was calculated using the SYNCSA v.1.3.3 (Debastiani & Pillar, 2012) in the R Statistical Environment (R Core Team, 2018).

Results

The first four PCPS axes, considering floodplain and lake scales, and the first three for subsystem scale explained each at least 5% of the total variation, and were thus used in modeling approaches.

At the floodplain scale the first four PCPS explained 58% of total variation, but only PCPS3 and 4 exhibited some model (OLS) better than the null model (Table 2). The best model for PCPS3 contained total phosphorous (Total-P) which exhibited significant results for both *site.shuffle* and *taxa.shuffle* null models, showing an association of Commelinids and Orchidaceae family with higher phosphorous values and Haloragaceae and Cabombaceae families with lower phosphorous values (Figure 1). The best model for PCPS4 contained total nitrogen (Total-N) which exhibited a significant result only for *site.shuffle*. In this case, relationship with nitrogen can be inferred only for the taxa, but it there are no consequences for phylogenetic clade definition considering this PCPS. Indeed, there is no clear relationship between larger clades and high or low nitrogen concentrations (Figure 1). The CWM traits of stem and root presence/absence exhibited the higher negative correlation ($r=-0.83$; $P<0.001$ and $r=-0.75$; $P<0.001$, respectively) with PCPS3 while the PCPS4 did not show strong correlations to any CWM trait (Supplementary Material 4).

At the subsystem scale, the first three PCPS explained 45% of total variation and all exhibited significant results for both *site.shuffle* and *taxa.shuffle* null models (Table 2). For PCPS1 the best model (GLS) contained the HL30. By aggregating taxa in higher clades, it is possible to observe that Commelinids, Polygonaceae and Orchidaceae occurred mainly when HL30 values were high, while Saxifragales and most of Rosids and Asterids species occurred at lower HL30 values (Figure 2). Fasciculate roots and leaf length showed the highest positive correlation with this phylogenetic dimension ($r=0.73$, $P<0.001$) (Supplementary Material 4). For PCPS2, the best model (GLS) contained the pH, showing an association of the ANA Grade (which include mainly Nympheales as aquatic taxa), Hydrocharitaceae and Alismataceae with higher pH values while all the other clades except Saxifragales, Ceratophyllales, and Amaranthaceae were associated with lower pH values. In line with higher clades, the

most related trait to PCPS2 was fixed submerged plants (r=0.82, P<0.001) (mostly represented in Hydrocharitaceae). The best model for PCPS3 contained the "subsystem" and "TIME" variables (Table 2), with Alismatales and Lamiales mostly occurring at the Baia subsystem and in early periods, while Rosids, Poaceae, Cyperaceae, Solanales, and Gentianales associated with recent periods and both Ivinhema and Paraná subsystems (Figure 3). Also, Cabombaceae seems to be associated particularly to Paraná and Polygonaceae and Nymphaeaceae to Ivinhema (Figure 3). Life form groups were also related to PCPS3, with free-floating species (r =0.71, P<0.001) and erect stem (r =0.71, P<0.001) having the highest positive correlation; while the leaf thickness (r =-0.78, P<0.001) showed the highest negative correlation (Supplementary Material 4).

At the lake scale, the first four PCPS explained 46% of total variation, and the first three showed some model better than the null model, but only for the *site.shuffle* (Table 2). The "subsystem" predictor was always present in best models, being the only one in some of the best models for PCPS2 and PCPS3. The "subsystem" and "TIME" variables were the predictors of the best model for PCPS1. For PCPS1, the Commelinids clade and Orchidaceae family were associated with early periods and in the Ivinhema subsystem, while the other clades were associated with recent periods and in the other subsystems (Figure 4). At the PCPS2 axis, the ANA grade (see above) was strongly associated to the Paraná subsystem (Figure 4); while the Hydrocharitaceae and Araceae families were strongly associated to the Baia subsystem considering PCPS3 (Figure 5). Fasciculate roots were positively correlated with PCPS1, free-floating species with PCPS3, and PCPS2 did not show any strong correlation (r > 0.7) to any CWM trait (Supplementary Material 4).

Table 2. Model selection results for each PCPS of aquatic macrophytes species at three spatial scales. Significant values are highlighted in bold for variables selected for the best model (see description of variables in methods). NS = non-significant.

Models	R^2	F-value	Permutation test	
			$P_{\text{site shuffle}}$	$P_{\text{taxa shuffle}}$
FLOODPLAIN				
PCPS1				
Null model	NS	NS	NS	NS
PCPS2				
HL30	NS	NS	NS	NS
PCPS3				
Total-P	0.19	8.76	**0.005**	**0.022**

PCPS4				
Total-N	0.12	4.96	**0.032**	0.136
SUBSYSTEM				
PCPS1				
HL30	0.55*	6.88	**0.011**	**0.019**
PCPS2				
pH	0.53*	11.85	**0.001**	**0.018**
PCPS3				
TIME + Subsystem	0.61	58.18	**<0.001**	**0.020**
LAKE				
PCPS1				
TIME + Subsystem	0.38	45.73	**<0.001**	0.404
PCPS2				
Subsystem	0.53*	21.46	**<0.001**	0.211
PCPS3				
Subsystem	0.57*	30.25	**<0.001**	0.071
PCPS4				
Null model	NS	NS	NS	NS

*Pseudo-R^2

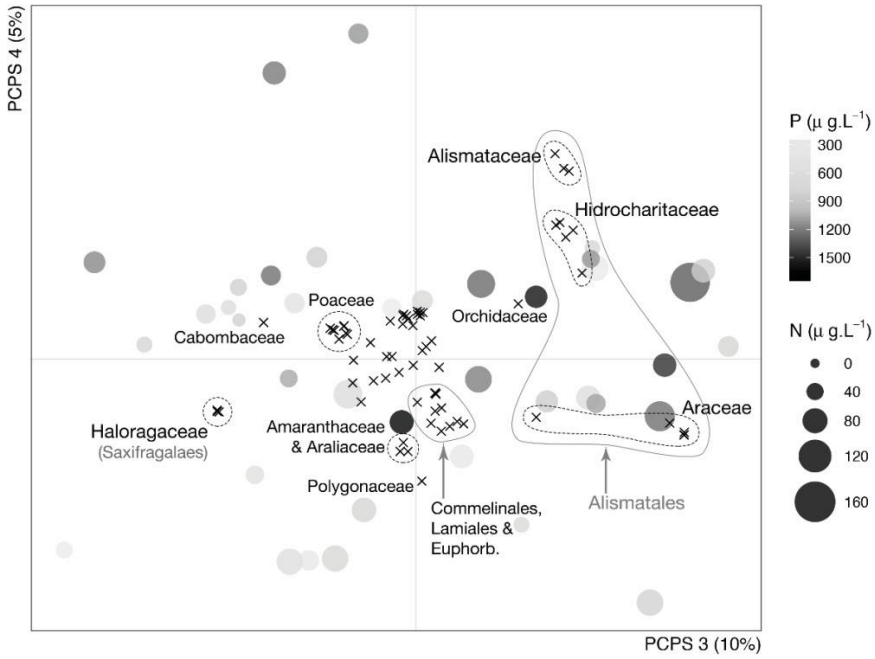


Figure 1. Scatter diagram of the third and fourth principal coordinates of phylogenetic structure of aquatic macrophytes species at floodplain scale occurring along P (significant for PCPS3)/N (significant for PCPS4) gradients of the Upper Paraná River floodplain. The 'x' symbols represent species with an indication of their phylogenetic clades or taxonomic family identity. P = Total phosphorous, N = Total nitrogen.

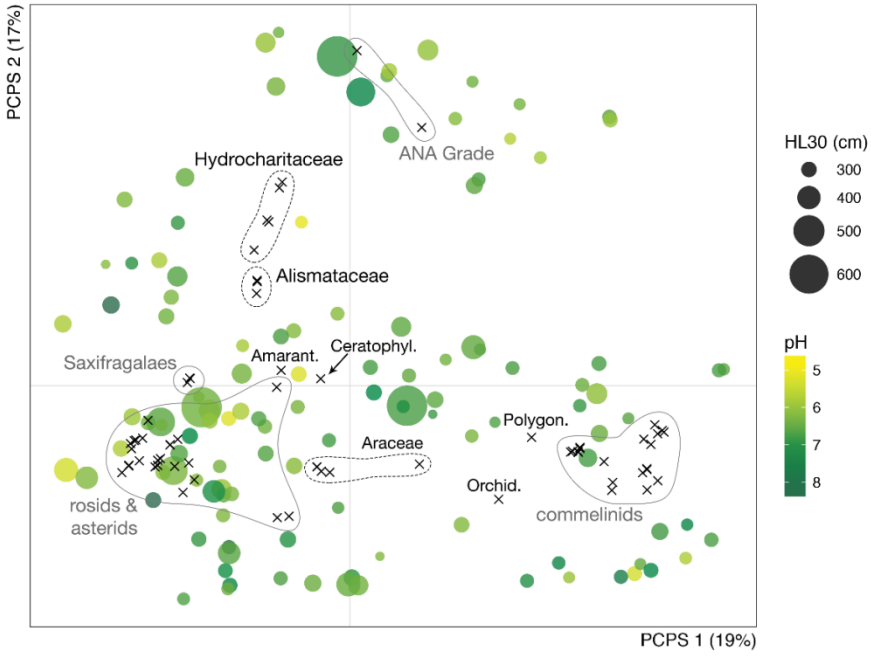
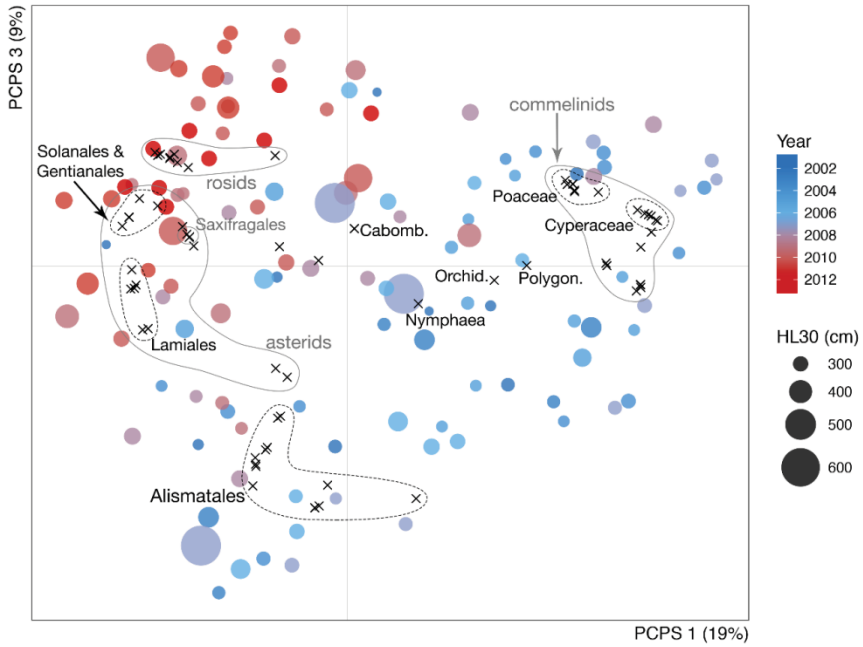


Figure 2. Scatter diagram of the first and second principal coordinates of phylogenetic structure of aquatic macrophytes species at the subsystem scale occurring along HL30 (significant for PCPS1)/pH (significant for PCPS2) gradients of the Upper Paraná River floodplain. The 'x' symbols represent species with an indication of their phylogenetic clades or taxonomic family identity. Abbreviated names represent families. HL30 = Hydrometric level 30 days before the sampling.



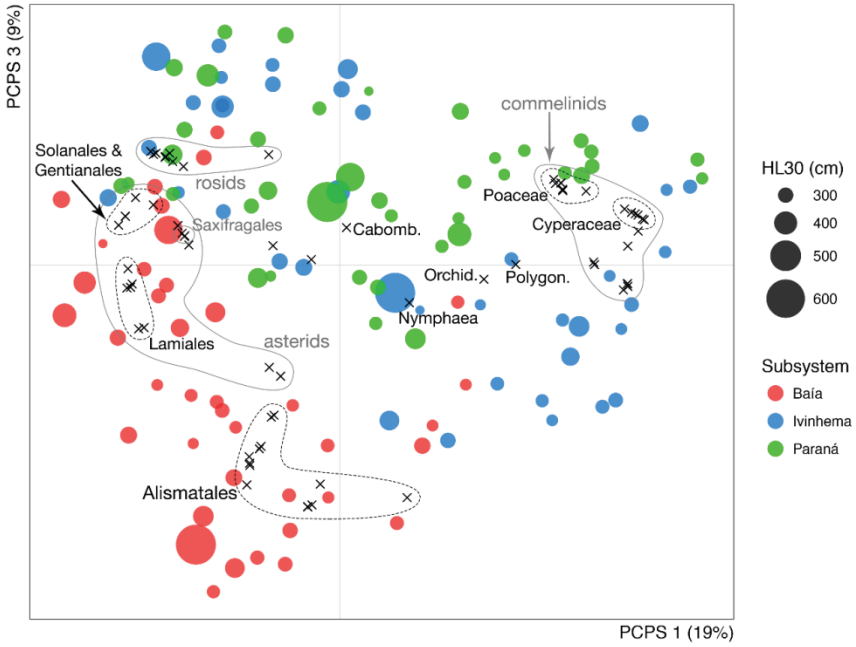


Figure 3. Scatter diagram of the first and third principal coordinates of phylogenetic structure (PCPS) of aquatic macrophytes species at the subsystem scale occurring along a HL30 (significant for PCPS1)/periods (upper) or subsystem (low; both significant for PCPS3) gradient of the Upper Paraná River floodplain. The 'x' symbols represent species with an indication of their phylogenetic clades or taxonomic family identity. Abbreviated names represent families. HL30 = Hydrometric level 30 days before the sampling.

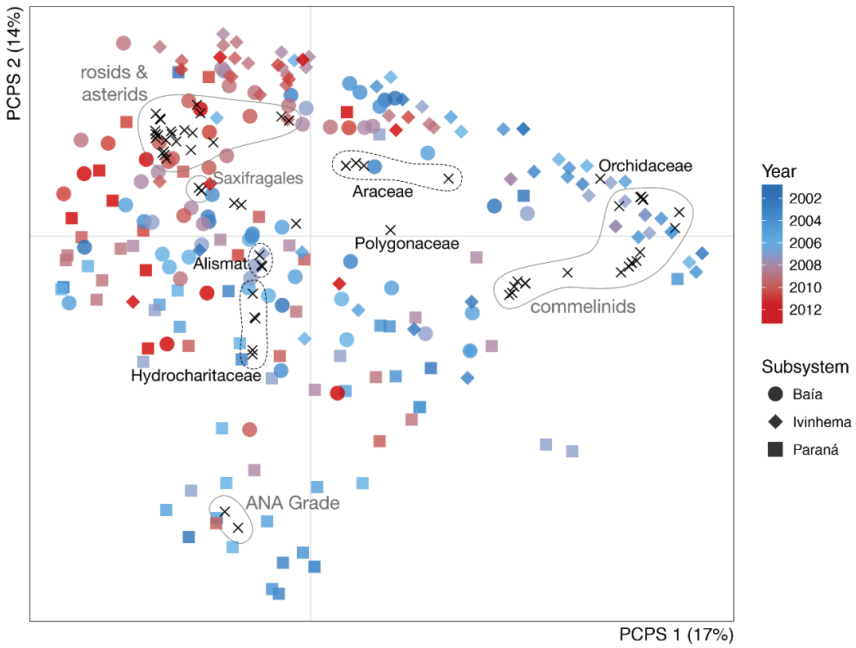


Figure 4. Scatter diagram of the first and second principal coordinate of phylogenetic structure of aquatic macrophytes species at lake scale along periods (significant for PCPS1)/subsystems (significant for PCPS1 and PCPS2) of the Upper Paraná River

floodplain. The ‘x’ symbols represent species with an indication of their phylogenetic clades or taxonomic family identity. Alismat. = Alismataceae family. Year = periods aggregated in years to facilitate visualization.

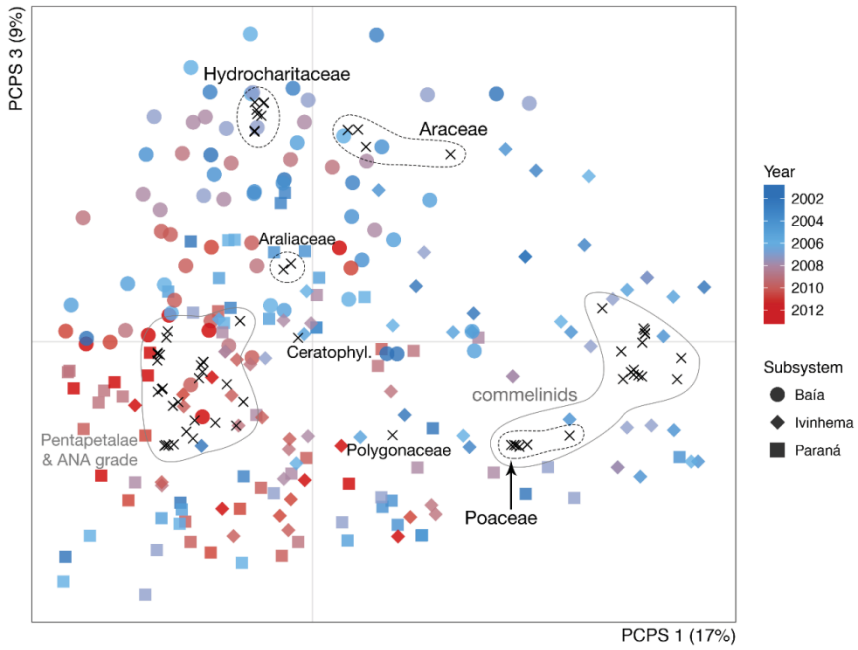


Figure 5. Scatter diagram of the first and third principal coordinate of phylogenetic structure (PCPS) of aquatic macrophytes species at lake scale periods (significant for PCPS1)/ subsystems (significant for PCPS1 and PCPS3) of the Upper Paraná River floodplain. The ‘x’ symbols represent species with an indication of their phylogenetic clades or taxonomic family identity. Ceratophyl. = Ceratophyllaceae family.

Discussion

Here, we explained the distribution of aquatic macrophytes in the UPRF over 38 periods (or 11 years). We have demonstrated the combined role of environmental filtering in species distribution with and without phylogenetic clades relatedness. We were also able to identify what such differentiation means for mean trait values of communities. We corroborated the expectation that mechanisms explaining distribution over time is dependent on spatial scale. Whatsoever we need to consider that the taxonomic bias registered in earlier studies at the UPRF could also contribute to such distributional pattern notice by us.

Firstly it is important to note that aquatic macrophyte distribution along the temporal gradients analyzed are non-random (*i.e.*, there were always better models than

the *site.shuffle* null model). Recent studies have used several approaches to explain aquatic community variation over gradients (see review in Heino et al., 2015 and references therein). An overall conclusion is that communities are poorly explained by proxies of environmental filtering, or proxies of among-site dispersal (if spatial variation is analyzed, see Heino et al., 2015). Indeed, this was the main conclusion for aquatic macrophytes in the UPRF (Padial et al., 2014). Here, we add to this knowledge by demonstrating that, even with a poor explanation of previous studies, taxa distribution is not random and can be explained by environmental predictors. Also, such distribution can be even reflected by phylogenetic structuring along gradients; *i.e.*, observed in our study particularly at the larger spatial scales, where models were better than *taxa.shuffle* null model.

The correlates of aquatic macrophytes distribution depended on the spatial scale, and interpretations are detailed below. However, it is interesting that the variable representing continuous temporal variation (TIME) was particularly important at local scales (considering subsystems and lakes as units) and a continuous change in species distribution may be interpreted as an "evolution" of the community. However it is important to consider that around 2007, an intensive review in taxa identification occurred resulting in the addiction of several species in the aquatic macrophyte list (Ferreira, Mormul, Thomaz, Pott & Pott, 2011). Therefore, temporal changes in aquatic macrophytes may be an artifact of this taxonomic identification bias. Surely, interpretations of temporal patterns in our study are thus affected by such bias, and we avoided reaching conclusions that may be a result of an artifact. However, it is interesting that other variables were important even at local scales.

Patterns at floodplain scale

At the coarser scale of our study, the temporal gradients did explain phylogenetic relatedness according to Total-P. At first, we could interpret this result as related to the fact that community is changing towards clades more adapted to high or low Total-P concentrations. Given the known oligotrophication reported at the UPRF (Roberto et al., 2009), we were induced to conclude that communities may be evolving toward species more tolerant to low phosphorus concentration. However, this would be true only if over the period analyzed, the Total-P was, in fact decreasing. The oligotrophication event occurred before our studied period, and is described comparing data from the 80' and the 90' with the time interval used here (see Figure 4 in Roberto

et al., 2009). Therefore, the correct interpretation of our result is that there were no Total-P continuous increase from 2002-2012, but specific periods with high and low concentrations have selected certain clades: indeed, it is possible to suggest higher classifications typical of high and low nutrients in Figure 2 (see also result description). We generated other evidences that nutrients are important to aquatic macrophytes structuring at floodplain scale, given that Total-N was also related to taxa distribution (but not reflected in phylogenetic structuring).

Nutrient concentration is indeed one of the main responsible for aquatic communities' structure (Lacoul & Freedman, 2006; Dar, Pandit & Ganai, 2014). At the scale studied by us, we found that stems and root presence/absence were positively related with phosphorous concentration. In line with this, Tabata et al. (2014) verified that the presence of root is an important trait to indicate nutrients assimilation; and Pereto et al. (2016) demonstrated that nutrient status of ecosystems determine leaf/root trade-off investment.

Interestingly, there was no relationship between aquatic macrophyte distribution and the variable indicating the hydrometric regime – HL30. The overall theory in floodplains is that flooding regime is the main driving force given that during floods, allochthonous nutrients are incorporated in water column (Junk et al., 1989, Neiff 1990, Thomaz et al., 2007). In the UPRF, flood regime has been long recognized as the major driving force of communities and ecosystems processes (see a review in Thomaz, Agostinho & Hahn, 2004). However, it is also recognized that dam operations have controlled flood pulses, resulting in strong consequences to nutrient inputs (Souza-Filho, 2009). Our results are in line with this, but suggest that nutrient concentrations (instead of hydrometric variables) seems to be the best proxy of community distribution at larger spatial scales considering long-term variation in a period in which floods are well controlled. Flood events indeed have an effect at biological communities' distribution (Padial et al., 2009), however, this effect is due to nutrient concentrations, which may indeed be main the aquatic biota resource.

Patterns at subsystem scale

When analyses consider subsystems as sampling units, its classification was an important predictor of community distribution, also reflected in phylogenetic relatedness. Indeed, several previous studies have clearly demonstrated that subsystem classification is a major environmental gradient that determine community

differentiation (Borges & Train, 2009; Padial et al., 2012). Community assembly in fact occurs in sites spatially heterogenous (Pillar & Duarte, 2010; Peres-Neto, Leibold & Dray, 2012; Spasojevic, Copeland & Suding, 2014; Cadotte & Tucker, 2017), such as the different subsystems of the UPRF. Stein, Gerstner & Kreft (2014) demonstrated that distinct sites could promote species coexistence, persistence and diversification. Indeed, classification in subsystems (summarizing a set of environmental and biological differences) is an important aspect in structuring aquatic macrophytes communities at lake scale.

We add to this knowledge by suggesting that structuring in subsystems is combined to temporal variation over the 11 years. It is clear that certain groups were more observed in earlier periods and others in later periods; which may be related to a known taxonomic bias in aquatic macrophyte identification at this floodplain (Ferreira et al., 2011). However, it is also clear that certain groups are more typical to certain subsystems: such as Alismatales and Lamiales to Baia, Cabombaceae to Paraná and Polygonaceae and Nymphaeaceae to Ivinhema (see Figure 3); which can also be further explored given that some traits (e.g. free-floating, erect stems and leaf thickness) were related to the aquatic macrophyte distribution mainly affected by subsystems.

At this scale, other variables were also important, such as HL30 for PCPS1 and pH for PCPS2. Indeed, it is possible to describe some groups more or less related to high and low values of hydrometric levels. It has already demonstrated that aquatic macrophytes community composition changes in response to strong short-term temporal variation after an extreme flood event (Padial et al., 2009). We corroborate previous results and add to the knowledge that this is reflected in phylogenetic structure according to hydrometric regime. There are aquatic plants with specific adaptations to fluctuation in water level, such as the fixed with floating leaves like water lilies (Gillespie, 2018). Indeed, Nymphaeaceae was one of the groups associated to those periods with high HL30, showing its adaptation to flood events.

Considering pH, it is difficult to find particular groups associated to high or low pH values, but it is already reported in literature the effect of pH concentration in certain aquatic macrophyte taxa (Catling, Freedman, Stewart, Kerekes & Lefkovitch, 1986) especially the submerged ones (Pereira, Trindade, Albertoni & Palma-Silva (2012). It is plausible to think that submerged and free floating species would be more related to low water pH concentrations given their main nutrient source are at the water column. Considering specifically submersed species, Isoetidea fit well in such scenario.

Therefore no Isoetidea was registered at the UPRF instead, Eloideides such as *Egeria najas*, *Egeria densa* and *Hydrilla verticillata* are present and use bicarbonate as carbon source in alkaline pH. Moreover, low pH concentrations directly affect phytoplankton occurrence which will guarantee water column transparency and submerged and/or free floating species occurrence (Camargo, Pezzato & Henry Silva, 2003). Since pH was an indicator of phylogenetic relatedness along the time, we need to consider that indeed such environmental variable also comes to explain communities' distribution considering phylogenetic relatedness (Villalobos, Carotenuto, Raia & Diniz-Filho, 2016). Since then, phylogenetic structure can be determined by trait conservation along different spatial scales and evolutionary relationships (Blomberg, Garland & Ives, 2003; Martins, Seger, Wiegand & Santos, 2018).

Patterns at lake scale

The environmental heterogeneity observed among subsystems was reflected at lake scale, given that community structure was explained by the variable indicating which subsystem each lake belongs. However, there was no evidence of phylogenetic structuring at this local scale, but only a community response to environmental gradients more than expected by a null model. A continuous temporal change in community structure was also observed at this scale. Environmental conditions indeed filter species along a longitudinal gradient coming from a regional pool where species only colonize habitats with similar environmental aspects from previous site (Boschilia, Oliveira & Schwarzbold, 2016). This is indeed expected for macrophytes among subsystems in UPRF, in line with previous studies (Padial et al., 2009; 2012). Interestingly, such pattern was observed at both lake and subsystem scale, showing that the sampling unit grain did not affect the clear effect of subsystems structuring aquatic macrophyte distribution.

Likewise, it is also important to consider that heterogeneity is generated over space and time (Padial et al., 2009; Padial et al., 2012; Boschilia et al., 2016). As also suggested by previous studies in UPRF, a continuous change in environmental conditions occurs (Roberto et al., 2009), which can also cause a continuous change in community structure. Interestingly, this is only observed at lake scale, suggesting that pooling lakes is sampling units of higher grains (subsystems or floodplain) may mask the temporal changes in community structure. This may occur given that temporal variation may depend on the "nature" of the lake: sampled lakes were not only from

different subsystems, but also differ given their connectivity to the main channel (see also Dittrich et al., 2017). As a consequence, the continuous temporal changes in the UPRF may not equal be in all habitats. In sense, one may wonder why the connectivity of the lake was not an important factor structuring macrophytes. Indeed, connectivity and habitat morphology are usually good predictors of macrophyte communities (Santos & Thomaz, 2007). The likely explanation is that the effect of connectivity may depend on the subsystem considering nutrient concentration, water flow, species propagules and lake distance from the river main channel, for example. Therefore, by integrating results at lake and subsystem scale, we suggest that subsystem classification is a more powerful to structure aquatic macrophyte community (see also Padial et al., 2012).

Species persistence in certain sites, even over long periods and strong environmental variation, indicates that resource use can continue due to a morpho-physiological adjustment of species. This is only possible if the carried traits enable plants to explore resources when they encounter a novel condition (Brooker, 2006). Aquatic macrophytes are particularly plastic considering their traits (Li, Geng & Lan, 2016), indicating that it is a group that may exhibit a high 'ecological fitting' (*sensu* Agosta & Klemens, 2008).

Relationship between distributions patterns and functional traits

More than describing and explaining distributional patterns of aquatic macrophytes, we also investigated how functional traits that are usually measured in macrophytes (e.g. Fu, Yuan, et al., 2018) relate to such patterns. We partially corroborated our hypothesis that related traits would be different according to the scale. At floodplain scale, when the community structuring of subsystems is ignored, the related traits were morphological ones (stem and root presence/absence), and associated to the distributional patterns along the phosphorous gradient. Although not causal, such relationship may suggest that only the few plants without roots and/or stems, such as *Wolffia* sp., *Wolfiella lingulata* and *Wolfiella oblonga*, seems to be affected by phosphorous concentrations.

On the other hand, at the scales that considered the subsystem classification on aquatic macrophyte distribution (i.e. subsystem and lake scales), the traits related to PCPSs affected by subsystem classification were mainly life forms. Therefore, our result suggests that in a scenario of strong environmental filtering (i.e. among subsystems), the selected species are either from different clades and life forms, even if

not phylogenetically structured (according to a null model at local scale). Aquatic macrophytes life forms were historically used to differ species according to their strategy in exploring resources (Beklioglu & Moss, 1996). With the recent popularity of functional ecology studies (Irschick et al., 2013) and methods to calculate functional diversity indexes, the choice of traits is at the same time central and polemic (Zhu et al., 2017). We indeed urge for future studies that may elucidate a better choice of traits to explain distribution of aquatic macrophytes. We suggest that a simple classification in life forms may be a good approach for aquatic plants (see also Schneider, Cunha, Marchese & Thomaz, 2018).

Even so, the macrophyte distribution over subsystems at the local scale was not only related to a life form trait, but also to a trait related to root morphology. Such trait is important to indicate how plants acquire nutrients (Tabata et al., 2015), and given the difference among subsystems considering nutrient availability (Roberto et al., 2009), it is indeed expected that a trait related to nutrient absorption could be important.

At subsystem scale, other traits were also related to distribution along gradients: i) leaf length according to a gradient of hydrometric level fluctuation; and ii) erect stem and leaf thickness to the temporal and subsystem gradients. As stated in two paragraphs above, such relationships are difficult to explain given that there are few studies exploring what functional traits of aquatic plants means considering their filtering in ecosystems (Gratani, 2014). Even so, a recent study have also related traits similar to the abovementioned (i.e., traits related to leaf and stem) to hydrological variation in a Chinese floodplain (Fu, Lou, et al., 2018).

Conclusions

Taking together, our results reinforce the relevance that long-term data indeed has in demonstrating species temporal and spatial patterns (Thomaz et al., 2009; Boschilia et al., 2016). In summary, we indicate that aquatic macrophytes community structure depends on environmental gradient and/or phylogenetic relatedness according to the spatial scale analyzed. Phylogenetic relatedness and consequence aquatic macrophyte distribution is usually explained by environmental gradients. Moreover, phylogenetic structuring can be observed at larger scales. Also, we generated evidence that aquatic macrophyte distribution occur mainly related to the difference among subsystems at local scales. This was reflected in plant traits that may represent different strategies of species to explore resources over the environmental gradients. Taking

together, we suggest that a simple classification in classic life forms is a fine initial strategy to understand how plants respond to environmental filtering. Indeed, it seems that such classification can also be reflected in clade distinctions at larger scales.

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Supplementary Material 1 Trait database for the aquatic macrophyte species sampled at the Upper Paraná River floodplain. Continuous traits are represented by mean values. Traits from literature: life form, persistence, blooming, pilosity, leaf consistency, root and stem architecture. Traits measured in field: height, leaf width, leaf length, leaf thickness, stem thickness, petiole length, root length, petiole, stem and root presence/absence.

SPECIES	LIFEFORM	PERSISTENCE	BLOOMING	PILOSITY	LEAF CONSISTENCY	ROOT ARCHITECTURE	STEM ARCHITECTURE	HEIGHT (cm)	LEAF WIDTH (cm)	LEAF LENGTH (cm)	LEAF THICKNESS (mm)	STEM THICKNESS (mm)	PETIOLE LENGTH (mm)	ROOT LENGTH (cm)	PETIOLE P/A	STEM P/A	ROOT P/A
Aeschynomene_sensitiva	Amphibian	Perennial	Annual	Glabrous	Herbaceous	Pivoting	Erect	250.0	1.10	7.75	0.06	2.45	0.40	75.00	1	1	1
Alternanthera_sp	Amphibian	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Prostrate	300.0	3.25	8.50	0.12	5.54	0.60	17.00	1	1	1
Azolla_sp	Free_floating	Annual	NA	Glabrous	Herbaceous	Fasciculated	NA	0.20	2.25	2.00	2.00	0.00	0.00	1.25	0	0	1
Bacopa_salzmannii	Amphibian	Annual	Annual	Glabrous	Coriaceous	Pivoting	Erect	20.00	0.90	1.35	0.57	0.68	0.00	2.00	0	1	1
Brachiaria_mutica	Amphibian	Perennial	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	110.0	3.50	25.0	0.28	1.00	0.00	9.00	0	1	1
Cabomba_caroliniana	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Prostrate	157.50	3.95	2.40	0.12	1.14	1.10	5.75	1	1	1
Cabomba_sp	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Prostrate	300.0	3.80	2.40	0.11	1.64	1.50	18.00	1	1	1
Caperonia_sp	Amphibian	Perennial	Monthly	Pilous	Herbaceous	Fasciculated	Erect	100.0	1.15	8.75	0.17	3.23	0.25	67.32	1	1	1
Ceratophyllum_demersum	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Pivoting	Prostrate	210.0	1.85	2.50	0.23	0.20	0.00	19.50	0	1	1
Chara_sp	Fixed_submerged	Perennial	NA	Glabrous	Herbaceous	Pivoting	Prostrate	30.00	0.35	5.75	0.09	1.00	0.00	9.25	0	1	1

Commelina_sp	Amphibian	Annual	Semester	Glabrous	Herbaceous	Fasciculated	Prostrate	75.00	1.43	9.25	0.13	1.98	0.00	6.50	0	1	1
Cuphea_sp	Amphibian	Annual	Annual	Glabrous	Herbaceous	Pivoting	Erect	175.0	2.50	9.50	0.28	3.50	5.50	10.00	1	1	1
Cyperus_sp	Amphibian	Annual	Monthly	Glabrous	Coriaceous	Fasciculated	Erect	98.00	1.76	34.0	0.35	6.89	0.00	9.25	0	1	1
Diodia_sp	Amphibian	Annual	Annual	Glabrous	Coriaceous	Pivoting	Erect	35.00	2.25	1.10	0.45	33.00	3.25	7.50	1	1	1
Echinodorus_sp	Emergent	Annual	Semester	Glabrous	Coriaceous	Fasciculated	Erect	140.0	18.1	18.5	0.46	6.62	29.0	13.50	1	1	1
Eclipta_alba	Amphibian	Annual	Semester	Pilous	Coriaceous	Pivoting	Erect	45.00	1.80	8.40	0.17	2.44	0.00	7.15	0	1	1
Egeria_densa	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Erect	195.0	0.14	1.49	0.16	1.13	0.00	5.75	0	1	1
Egeria_najas	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Pivoting	Erect	250.0	0.15	1.50	0.18	1.11	0.00	5.00	0	1	1
Eichhornia_azurea	Fixed_floating	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Prostrate	58.00	24.0	12.5	0.60	16.50	180.0	57.50	1	1	1
Eichhornia_crassipes	Free_floating	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Prostrate	59.00	7.75	12.5	0.60	12.50	240.0	42.75	1	1	1
Eleocharis_sp	Emergent	Perennial	Annual	Glabrous	Herbaceous	Fasciculated	Erect	24.00	0.72	22.7	0.20	2.05	0.00	5.13	0	1	1
Fuirena_sp	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Prostrate	85.00	1.05	12.5	0.11	4.30	12.80	6.75	1	1	1
Habenaria_sp	Emergent	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Erect	35.00	1.85	17.5	0.18	2.90	0.00	15.00	0	1	1
Hibiscus_sp	Amphibian	Perennial	Semester	Pilous	Herbaceous	Fasciculated	Erect	180.00	8.80	15.6	0.28	3.55	21.75	11.75	1	1	1
Hydrilla_verticillata	Fixed_submerged	Perennial	Semester	Glabrous	Herbaceous	Fasciculated	Erect	450.0	0.55	2.05	0.14	1.12	0.00	5.95	0	1	1
Hydrocotyle_sp	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	9.63	6.02	2.68	0.23	1.78	82.10	16.45	1	1	1
Hydrocotyle_ranunculoides	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	9.05	5.78	2.20	0.17	1.75	76.56	15.40	1	1	1
Hydrolea_spinosa	Amphibian	Perennial	Annual	Pilous	Herbaceous	Pivoting	Prostrate	75.00	1.55	9.75	0.17	8.50	20.00	16.00	1	1	1
Hygrophila_costata	Amphibian	Annual	Annual	Pilous	Herbaceous	Pivoting	Erect	110.0	2.15	10.3	0.16	2.82	0.00	12.50	0	1	1
Hymenachne_amplexicaulis	Emergent	Perennial	Annual	Glabrous	Herbaceous	Fasciculated	Prostrate	175.00	3.60	30.0	0.17	10.25	0.00	17.50	0	1	1
Hyptis_sp	Amphibian	Annual	Semester	Pilous	Herbaceous	Pivoting	Erect	110.0	3.20	8.40	0.24	2.05	0.74	17.50	1	1	1

Ipomoea_sp	Epiphyte	Perennial	Annual	Pilous	Herbaceous	Pivoting	Erect	187.50	3.85	7.18	0.21	3.60	3.10	13.75	1	1	1
Leersia_hexandra	Amphibian	Perennial	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	110. 0	2.90	11.0	0.45	4.85	0.00	7.80	0	1	1
Lemna_valdiviana	Free_floating	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	NA	0.02	0.03	0.04	0.18	0.00	0.00	0.65	0	0	1
Limnobium_laevigatum	Free_floating	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Prostrate	6.50	3.85	3.85	4.65	2.65	44.00	33.00	1	1	1
Limnocharis_sp	Emergent	Annual	Semester	Glabrous	Coriaceous	Fasciculated	Erect	42.50	14.5	21.0	0.18	13.50	12.80	16.50	1	1	1
Lindernia_rotundifolia	Fixed_submerged	Annual	Annual	Glabrous	Coriaceous	Pivoting	Erect	25.00	2.30	3.10	0.17	1.88	0.80	8.25	1	1	1
Ludwigia_helminthorrhiza	Amphibian	Perennial	Annual	Glabrous	Coriaceous	Pivoting	Prostrate	3.10	3.60	3.55	0.30	4.75	12.50	10.25	1	1	1
Ludwigia_leptocarpa	Amphibian	Annual	Semester	Pilous	Herbaceous	Pivoting	Erect	150.0	3.43	13.5	0.12	4.50	4.00	23.00	1	1	1
Ludwigia_sp	Amphibian	Annual	Annual	Pilous	Herbaceous	Pivoting	Erect	146.25	1.32	8.06	0.12	3.13	4.71	16.88	1	1	1
Mimosa_setosa	Amphibian	Perennial	Semester	Glabrous	Herbaceous	Pivoting	Erect	160.0	0.45	1.45	0.16	5.00	5.50	85.00	1	1	1
Myriophyllum_brasiliensis	Fixed_submerged	Annual	Semester	Glabrous	Coriaceous	Pivoting	Erect	100.0	1.25	2.40	0.18	1.00	4.45	12.00	1	1	1
Myriophyllum_matogrossense	Fixed_submerged	Annual	Semester	Glabrous	Coriaceous	Pivoting	Erect	80.00	4.25	2.90	0.18	1.00	3.20	12.00	1	1	1
Myriophyllum_sp	Fixed_submerged	Annual	Semester	Glabrous	Coriaceous	Pivoting	Erect	50.00	0.45	2.55	0.24	0.87	4.00	16.00	1	1	1
Najas_microcarpa	Fixed_submerged	Annual	Monthly	Glabrous	Coriaceous	Pivoting	Erect	42.50	0.28	2.25	0.13	0.95	0.00	5.50	0	1	1
Nitella_furcata	Fixed_submerged	Annual	NA	Glabrous	Herbaceous	Pivoting	Erect	30.00	0.40	3.40	0.50	1.00	0.00	11.00	0	1	1
Nymphaea_amazonum	Fixed_floating	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Prostrate	250.0	22.5	22.5	0.58	45.00	250.0	19.50	1	1	1
Nymphoides_indica	Fixed_floating	Perennial	Semester	Glabrous	Coriaceous	Pivoting	Prostrate	37.50	7.90	7.75	0.29	34.00	15.00	87.50	1	1	1
Oxycaryum_cubense	Emergent	Annual	Monthly	Glabrous	Coriaceous	Fasciculated	Prostrate	55.00	2.37	67.5	0.22	1.95	0.00	7.75	0	1	1
Panicum_sp	Emergent	Annual	Monthly	Pilous	Herbaceous	Fasciculated	Erect	125.0	0.40	16.0	0.14	1.16	0.00	15.75	0	1	1
Paspalum_sp	Emergent	Annual	Semester	Pilous	Herbaceous	Fasciculated	Erect	20.00	3.75	13.7	0.10	0.50	0.00	16.80	0	1	1
Paspalum_repens	Emergent	Annual	Semester	Pilous	Herbaceous	Fasciculated	Erect	22.50	4.50	14.0	0.12	0.45	0.00	17.50	0	1	1

Pistia_stratiotes	Free_floating	Annual	Annual	Pilous	Coriaceous	Fasciculated	Prostrate	32.50	5.65	10.0	0.35	2.25	0.20	25.00	1	1	1
Polygonum_sp	Emergent	Perennial	Annual	Pilous	Herbaceous	Pivoting	Erect	107.92	2.73	14.1	0.23	13.64	18.59	17.64	1	1	1
Pontederia_cordata	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	110.0	7.25	19.0	0.20	42.50	59.00	20.50	1	1	1
Pontederia_parviflora	Emergent	Perennial	Annual	Glabrous	Coriaceous	Fasciculated	Erect	95.00	6.95	21.5	0.17	38.50	51.50	22.00	1	1	1
Pontederia_triflora	Emergent	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Erect	75.00	2.75	6.15	0.11	33.50	4.85	16.00	1	1	1
Rhynchospora_sp	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Pivoting	Erect	110. 0	0.68	49.2	0.32	4.11	0.00	8.13	0	1	1
Ricciocarpus_natans	Free_floating	Annual	NA	Glabrous	Herbaceous	Fasciculated	NA	0.30	0.55	1.25	2.75	0.00	0.00	0.55	0	0	1
Rhynchanthera_sp	Amphibian	Annual	Semester	Pilous	Herbaceous	Pivoting	Erect	195.0	3.40	6.25	0.16	14.50	12.80	18.50	1	1	1
Sagittaria_sp	Emergent	Annual	Semester	Glabrous	Herbaceous	Fasciculated	Erect	85.00	7.50	27.0	0.93	22.50	405.00	35.00	1	1	1
Salvinia_sp	Free_floating	Annual	NA	Pilous	Herbaceous	Fasciculated	Prostrate	1.03	1.68	1.47	0.72	0.08	0.15	3.55	1	1	1
Scleria_gaertneri	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Erect	70.00	3.29	15.0	0.26	1.35	0.00	6.75	0	1	1
Solanum_glaucophyllum	Amphibian	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Erect	150.0	1.60	2.25	0.27	0.19	1.05	18.50	1	1	1
Solanum_sp	Amphibian	Perennial	Monthly	Glabrous	Herbaceous	Pivoting	Erect	148.0	1.15	2.14	0.25	0.18	1.00	17.60	1	1	1
Thalia_geniculata	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Pivoting	Erect	325.0	6.50	45.0	0.21	150.0	925.0	21.50	1	1	1
Thelypteris_interrupta	Amphibian	Perennial	NA	Glabrous	Coriaceous	Fasciculated	Prostrate	85.00	1.55	13.0	0.09	3.17	12.80	6.50	1	1	1
Typha_domingensis	Amphibian	Perennial	Semester	Glabrous	Coriaceous	Fasciculated	Erect	300.0	1.75	125.	0.62	35.00	0.00	55.00	0	1	1
Urochloa_arrecta	Amphibian	Annual	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	110.0	1.75	11.5	0.18	0.35	0.00	17.50	0	1	1
Urochloa_sp	Amphibian	Annual	Semester	Pilous	Herbaceous	Fasciculated	Prostrate	114.0	1.50	10.8	0.15	0.34	0.00	16.30	0	1	1
Utricularia_foliosa	Free_submerged	Annual	Annual	Glabrous	Herbaceous	Fasciculated	Prostrate	32.50	9.60	13.5	2.07	0.11	15.75	16.75	1	1	1
Utricularia_gibba	Free_submerged	Annual	Annual	Glabrous	Herbaceous	Fasciculated	Prostrate	16.00	4.75	5.66	0.10	0.03	0.00	1.75	0	1	1
Wolffia_sp	Free_floating	Annual	NA	Glabrous	Herbaceous	NA	NA	0.02	0.25	1.00	0.50	0.00	0.00	0.00	0	0	0

Wolfiella_lingulata	Free_floating	Annual	Semester	Glabrous	Herbaceous	NA	NA	0.02	0.17	0.28	0.20	0.00	0.00	0.00	0	0	0
Wolfiella_oblonga	Free_floating	Annual	Monthly	Glabrous	Herbaceous	NA	NA	0.02	0.05	0.38	0.20	0.00	0.00	0.00	0	0	0

Supplementary Material 2 Phylogenetic tree in newick format based on the phylogenetic hypothesis of Smith & Brown (2018), which was reconstructed based on data from GenBank and the Open Tree of Life taxa with a backbone and age estimates provided by Magallón et al. (2015) (ALLMB tree file).

(((((((caperonia_sp:115.786023,(aeschynomene_sensitiva:77.963161,mimosa_setosa:77.96317):37.822728)mrcaott2ott371:2.793039,(hibiscus_sp:116.378559,(rhynchanthera_sp:93.319489,(cuphea_sp:72.635862,(ludwigia_sp:18.86776,ludwigia_leptocarpa:18.86776,ludwigia_helminthorrhiza:18.86776):53.7681):20.683641):23.059108)mrcaott96ott1276:2.200511)rosids:3.826488,(myriophyllum_aquaticum:18.3721186,myriophyllum_sp:18.37212,myriophyllum_mattogrossensis:18.37212):104.0336482)mrcaott2ott2464:1.329145,(((((hyptis_sp:47.271421,(hygrophila_costata:43.420834,(utricularia_gibba:29.853637,utricularia_foliosa:29.85364):13.567194):3.850588):5.661324,bacopa_salzmannii:52.932738,lindernia_rotundifolia:52.932128):36.818716,(diodia_sp:85.913499,(hydrolea_spinosa:79.242394,((solanum_glaucophyllum:13.732431,solanum_sp:13.73243):52.917374,ipomoea_sp:66.649812):12.592582)Solanales.rn.d8s.tre:6.67142)mrcaott1191ott2192:3.837931)mrcaott248ott1191:16.990343,((eclipta_prostrata:68.269327,nymphoides_indica:68.269324):25.460992,(hydrocotyle_ranunculoides:12.804016,hydrocotyle_sp:12.804017):80.926208)mrcaott320ott1673:13.011199)mrcaott248ott320:13.132823,(alternanthera_sp:107.051286,polygonum_sp:107.051288)Caryophyllales.rn.d8s.tre:12.823146)mrcaott248ott557:3.860003)Pentapetalae:10.688948,ceratophyllum_demersum:134.423418)mrcaott2ott10930:1.33488,(((((commelina_sp:68.547999,((eichhornia_azurea:9.092223,eichhornia_crassipes:9.092223):0.047648,(pontederia_cordata:1.851647,pontederia_parviflora:1.85165,pontederia_triflora:1.85165):7.288223):59.408125)Commelinales.rn.d8s.tre:11.255471,thalia_geniculata:79.803928)mrcaott121ott3449:26.930401,((((((panicum_sp:14.194198,(urochloa_arrecta:6.620071,urochloa_mutica:6.62007,urochloa_sp:6.62005):7.574139):6.624881,((paspalum_sp:3.76418,paspalum_repens:3.76418):8.982464,hymenachne_amplexicaulis:12.746645):8.072448):18.931969,leersia_hexandra:39.75106):49.33125,xyris_sp:89.082311):4.739179,(((((cyperus_sp:8.812364,oxycaryum_cubense:8.812365):11.585018,fuirena_sp:20.397376):2.861776,eleocharis_sp:23.259157):6.652065,rhynchospora_sp:29.911219):11.242044,scleria_gaertneri:41.1526904):52.66822):7.154022,typha_domingensis:100.975511)Poales.rn.d8s.tre:5.758666)mrcaott121ott252:7.866937,habenaria_sp:114.600635)mrcaott1

21ott334:16.198196,(((((egeria_densa:5.450183,egeria_najas:5.450183):35.150371,limnobium_laevigatum:40.600555):4.343259,(najas_microcarpa:44.121916,hydrilla_verticillata:44.121928):0.821885):27.110915,((sagittaria_sp:33.56794,echinodorus_sp:33.567932):5.303396,limnocharis_sp:38.871318):33.183412):56.806627,((lemna_valdiviana:58.920125,(wolffia_sp:35.921223,(wolffiella_lingulata:1.022871,wolffiella_oblonga:1.022871):34.898353):22.998903):62.730604,pistia_stratiotes:121.650729):7.210626)Alismatales.rn.d8s.tre:1.937391)mrcaott121ott290:4.959306)mrcaott2ott121:3.206956,(nymphaea_amazonum:109.574466,(cabomba_caroliniana:23.336353,cabomba_sp:23.336363):86.238115):29.391074)mrcaott2ott2645;

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Supplementary Material 3 – Environmental models considering the environmental gradient on species distribution along the 38 sampling periods in the Upper Paraná River Floodplain applied for three spatial scales (Floodplain, Subsystem and Lake). All models were considered for: ordinary least squares (OLS) models and generalized least squares (GLS) models; all PCPS lower than the null model depending on the spatial scale and through the temporal autocorrelation covariate (corCAR1). TotalP = mean phosphorous concentration; TotalN = mean nitrogen concentration; YEAR = 38 periods; Turb. = turbidity; ISM = inorganic suspended material; HL30 = hydrometric level 30 days before the sampling; Temp. = temperature; pH= potential of hydrogen; Subsystem = subsystems analyzed at the study (Baia, Paraná and Ivinhema); Isolation = lake condition in relation to main channel, if isolated or not.

FLOODPLAIN SCALE

(PCPS ~ null)	(PCPS ~ Temp. + TotalP + TotalN)
(PCPS ~ YEAR + TotalP + TotalN)	(PCPS ~ Temp. + HL30)
(PCPS ~ YEAR + Temp.)	(PCPS ~ Temp.)
(PCPS ~ YEAR + Turb.)	(PCPS ~ pH + Temp.)
(PCPS ~ YEAR + ISM + Turb.)	(PCPS ~ pH)
(PCPS ~ YEAR + ISM)	(PCPS ~ Turb. + TotalN)
(PCPS ~ YEAR + HL30)	(PCPS ~ Turb. + Temp.)
(PCPS ~ YEAR)	(PCPS ~ Turb. + ISM)
(PCPS ~ TotalP + TotalN)	(PCPS ~ Turb. + HL30)
(PCPS ~ TotalP + ISM)	(PCPS ~ Turb.)
(PCPS ~ TotalP + Temp.)	(PCPS ~ ISM + TotalN)
(PCPS ~ TotalP + TotalN + ISM)	(PCPS ~ ISM)
(PCPS ~ TotalP)	(PCPS ~ HL30 + TotalP + TotalN)
(PCPS ~ TotalN + ISM)	(PCPS ~ HL30)
(PCPS ~ TotalN + Temp.)	
(PCPS ~ TotalN)	

SUBSYSTEM SCALE

(PCPS ~ null)	(PCPS ~ Temp. + TotalP + TotalN)	(PCPS ~ subsystem)
(PCPS ~ YEAR + TotalP + TotalN)	(PCPS ~ Temp. + HL30)	(PCPS ~ subsystem + TotalN)
(PCPS ~ YEAR + Temp.)	(PCPS ~ Temp.)	(PCPS ~ subsystem + TotalP)
(PCPS ~ YEAR + Turb.)	(PCPS ~ pH + Temp.)	(PCPS ~ subsystem + Turb.)
(PCPS ~ YEAR + ISM + Turb.)	(PCPS ~ pH)	(PCPS ~ subsystem + pH)
(PCPS ~ YEAR + ISM)	(PCPS ~ Turb. + TotalN)	(PCPS ~ subsystem + Temp. + Turb.)
(PCPS ~ YEAR + HL30)	(PCPS ~ Turb. + Temp.)	(PCPS ~ subsystem + ISM)
(PCPS ~ YEAR)	(PCPS ~ Turb. + ISM)	(PCPS ~ subsystem + YEAR)
(PCPS ~ TotalP + TotalN)	(PCPS ~ Turb. + HL30)	(PCPS ~ subsystem + HL30)
(PCPS ~ TotalP + ISM)	(PCPS ~ Turb.)	
(PCPS ~ TotalP + Temp.)	(PCPS ~ ISM + TotalN)	
(PCPS ~ TotalP + TotalN + ISM)	(PCPS ~ ISM)	
(PCPS ~ TotalP)	(PCPS ~ HL30 + TotalP + TotalN)	
(PCPS ~ TotalN + ISM)	(PCPS ~ HL30)	
(PCPS ~ TotalN + Temp.)		
(PCPS ~ TotalN)		

LAKE SCALE

(PCPS ~ null)	(PCPS ~ Turb. + ISM)
(PCPS ~ YEAR + TotalP + TotalN)	(PCPS ~ Turb.)
(PCPS ~ YEAR + Temp.)	(PCPS ~ ISM + TotalN)
(PCPS ~ YEAR + Turb.)	(PCPS ~ ISM)
(PCPS ~ YEAR +ISM + Turb.)	(PCPS ~ subsystem)
(PCPS ~ YEAR +ISM)	(PCPS ~ subsystem + TotalN)
(PCPS ~ YEAR)	(PCPS ~ subsystem + TotalP)
(PCPS ~ TotalP + TotalN)	(PCPS ~ subsystem + Turb.)
(PCPS ~ TotalP + ISM)	(PCPS ~ subsystem + pH)
(PCPS ~ TotalP + Temp.)	(PCPS ~ subsystem + Temp. + Turb.)

(PCPS ~ TotalP +TotalN + ISM)	(PCPS ~ subsystem + ISM)
(PCPS ~ TotalP)	(PCPS ~ subsystem + YEAR)
(PCPS ~ TotalN + ISM)	(PCPS ~ isolation + TotalN)
(PCPS ~ TotalN + Temp.)	(PCPS ~ isolation + TotalP)
(PCPS ~ TotalN)	(PCPS ~ isolation + TotalN + TotalP)
(PCPS ~ Temp. + TotalP + TotalN)	(PCPS ~ isolation + subsystem)
(PCPS ~ Temp.)	(PCPS ~ isolation + Turb.)
(PCPS ~ pH + Temp.)	(PCPS ~ isolation + ISM)
(PCPS ~ pH)	(PCPS ~ isolation + pH)
(PCPS ~ Turb. + TotalN)	(PCPS ~ isolation + Temp.)
(PCPS ~ Turb. + Temp.)	

Supplementary Material 4 - Correlation results (*r*) between each Principal Coordinate of Phylogenetic Structure (PCPS) exhibiting significant results for the pcps.sig tests with the community weighted means traits at its respective spatial scale (floodplain, subsystem, and lake). Significant results ($P \leq 0.05$) are highlighted in bold and strong correlations values ($r \geq 0.7$) filled with gray color.

Traits	FLOODPLAIN				SUBSYSTEM						LAKE					
	PCPS3		PCPS4		PCPS1		PCPS2		PCPS3		PCPS1		PCPS2		PCPS3	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Amphibian	-0.079	0.634	0.129	0.435	-0.405	**<0.001**	-0.294	**0.001**	0.653	**<0.001**	-0.370	**<0.001**	0.311	**<0.001**	-0.475	**<0.001**
Free floating	0.680	**<0.001**	-0.411	**0.009**	0.032	0.734	-0.448	**<0.001**	-0.805	**<0.001**	0.343	**<0.001**	0.416	**<0.001**	0.714	**<0.001**
Fixed submerged	-0.565	**<0.001**	0.148	0.369	-0.194	**0.036**	0.827	**<0.001**	0.217	**0.019**	-0.306	**<0.001**	-0.594	**<0.001**	0.138	**0.037**
Emergent	0.143	0.385	0.234	0.152	0.645	**<0.001**	-0.228	**0.014**	0.093	0.320	0.368	**<0.001**	-0.070	0.293	-0.347	**<0.001**
Fixed floating	-0.019	0.908	-0.224	0.170	0.561	**<0.001**	0.327	**<0.001**	-0.148	0.111	0.228	**0.001**	-0.554	**<0.001**	-0.068	0.303
Epiphyte	-0.433	**0.006**	0.178	0.277	-0.340	**<0.001**	-0.104	0.264	0.423	**<0.001**	-0.230	**<0.001**	0.149	0.025	-0.264	**<0.001**
Free submerged	0.246	0.131	-0.256	0.116	-0.254	**0.006**	0.119	0.200	-0.537	**<0.001**	-0.289	**<0.001**	0.078	0.243	0.264	**<0.001**
Perennial	-0.170	0.300	0.184	0.261	0.346	**<0.001**	0.316	**0.001**	0.356	**<0.001**	0.231	**<0.001**	-0.328	**<0.001**	-0.127	0.056
Annual	0.115	0.484	-0.186	0.258	0.102	0.273	-0.378	**<0.001**	-0.408	**<0.001**	0.093	0.159	0.215	**0.001**	-0.045	0.497
Annual blooming	0.256	0.116	-0.088	0.595	0.169	0.068	-0.637	**<0.001**	-0.144	0.120	0.322	**<0.001**	0.532	**<0.001**	-0.004	0.956
Semester blooming	-0.669	**<0.001**	0.387	**0.015**	-0.151	0.104	0.424	**<0.001**	0.428	**<0.001**	-0.235	**<0.001**	-0.358	**<0.001**	-0.304	**<0.001**
Monthly blooming	0.413	**0.009**	-0.384	**0.016**	0.445	**<0.001**	0.195	**0.035**	-0.139	0.135	0.075	0.262	-0.361	**<0.001**	-0.083	0.210
Glabrous	-0.071	0.668	-0.015	0.926	0.030	0.748	0.232	**0.012**	0.006	0.946	0.084	0.205	-0.129	0.051	0.073	0.272

Pilous	-0.137	0.405	-0.015	0.927	0.091	0.331	-0.336	**<0.001**	0.412	**<0.001**	-0.098	0.141	0.126	0.058	-0.560	**<0.001**
Herbaceous	0.335	**0.037**	-0.028	0.864	-0.238	**0.010**	0.483	**<0.001**	0.350	**<0.001**	-0.533	**<0.001**	-0.351	**<0.001**	-0.422	**<0.001**
Coriaceous	-0.289	0.074	-0.016	0.923	0.345	**<0.001**	-0.444	**<0.001**	-0.333	**<0.001**	0.590	**<0.001**	0.306	**<0.001**	0.391	**<0.001**
Pivoting	-0.182	0.269	0.087	0.599	-0.644	**<0.001**	0.018	0.846	0.576	**<0.001**	-0.679	**<0.001**	0.021	0.754	-0.516	**<0.001**
Fasciculated	-0.007	0.967	0.030	0.858	0.734	**<0.001**	0.003	0.976	-0.389	**<0.001**	0.720	**<0.001**	-0.048	0.473	0.361	**<0.001**
Erect stem	-0.196	0.232	0.286	0.078	-0.207	**0.025**	-0.065	0.485	0.713	**<0.001**	-0.273	**<0.001**	0.033	0.617	-0.606	**<0.001**
Prostrate stem	-0.204	0.212	-0.150	0.361	0.390	**<0.001**	0.247	**0.007**	-0.417	**<0.001**	0.266	**<0.001**	-0.178	**0.007**	0.282	**<0.001**
Petiole	-0.660	**<0.001**	0.033	0.840	-0.270	**0.003**	0.041	0.664	-0.096	0.305	-0.231	**<0.001**	0.226	**0.001**	0.052	0.438
Stem	-0.833	**<0.001**	0.311	0.054	0.152	0.101	0.348	**<0.001**	0.655	**<0.001**	-0.013	0.842	-0.308	**<0.001**	-0.599	**<0.001**
Root	-0.754	**<0.001**	0.325	**0.044**	0.199	**0.031**	0.264	**0.004**	0.665	**<0.001**	0.052	0.435	-0.267	**<0.001**	-0.594	**<0.001**
Height	-0.503	**0.001**	0.477	**0.002**	-0.162	0.080	0.608	**<0.001**	0.623	**<0.001**	-0.443	**<0.001**	-0.439	**<0.001**	-0.466	**<0.001**
Leaf width	0.016	0.924	0.160	0.329	0.479	**<0.001**	0.161	0.084	-0.409	**<0.001**	0.296	**<0.001**	-0.321	**<0.001**	0.132	0.047
Leaf length	-0.114	0.491	0.278	0.086	0.737	**<0.001**	-0.213	**0.021**	0.273	**0.003**	0.673	**<0.001**	-0.132	**0.046**	-0.270	**<0.001**
Leaf thickness	0.262	0.107	-0.388	0.015	-0.226	**0.014**	0.028	0.763	-0.783	**<0.001**	-0.121	0.068	0.040	0.548	0.577	**<0.001**
Stem thickness	-0.408	**0.010**	0.021	0.897	0.402	**<0.001**	-0.038	0.684	0.156	0.093	0.194	**0.003**	-0.228	**0.001**	-0.304	**<0.001**
Petiole length	-0.341	**0.034**	-0.095	0.565	0.426	**<0.001**	-0.248	**0.007**	-0.208	**0.024**	0.501	**<0.001**	0.012	0.863	0.094	0.156
Root length	-0.302	0.061	-0.236	0.149	0.100	0.282	-0.353	**<0.001**	0.188	**0.043**	0.299	**<0.001**	0.326	**<0.001**	-0.067	0.313

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